

# ON *PTERUCHUS* A MICROSPOROPHYLL OF THE CORYSTOSPERMACEAE

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# ON *PTERUCHUS* A MICROSPOROPHYLL OF THE CORYSTOSPERMACEAE

By J. A. TOWNROW

## SYNOPSIS

Three species of *Pteruchus* are redescribed, *P. africanus* Thomas, the type species, *P. dubius* Thomas and *P. simmondsi* (Shirley) Thomas. The material comes from Burnera Waterfall, Upper Umkomaas, Natal, and is of Molteno (Middle Triassic) age. A number of species are merged with *P. africanus*. The specimen originally named *Pteruchus edwardsi* Thomas is transferred to *Stachyopitys*. The ascription of *Pteruchus* to the *Dicroidium-Xylopteris* group of leaves, and the morphology of *Pteruchus*, are discussed. *Pteruchus* is compared with a number of other pollen organs, but is distinct from all.

## INTRODUCTION

*Pteruchus* was first described as a separate genus by Dr. H. Hamshaw Thomas (1933). He believed it to be the pollen organ of the extremely abundant Triassic forking leaves here called the *Dicroidium-Xylopteris* group. This term is meant to include the ten or so leaf-species placed in *Dicroidium* (Jakob & Jakob, 1950; Townrow, 1957) and the three species of *Xylopteris* (Jones & Jersey, 1947 under the name *Stenopteris*, and also p. 308). New information is now brought forward which strongly supports some of Thomas' conclusions, particularly the ascription of *Pteruchus* to the *Dicroidium-Xylopteris* group; but is against some other of his views, e.g. the limits of the several species of *Pteruchus*. It enables one to take up a definite stand on some points, in particular, on the morphology of *Pteruchus* which Dr. Hamshaw Thomas was obliged to leave uncertain.

The material examined consists of Thomas' material, and further more abundant specimens from the same locality, that is, from the Burnera Waterfall, Upper Umkomaas, Natal. This locality falls within the Molteno, and is of Middle Triassic age (Townrow, 1957 : 30, 31).

All type and figured specimens of *Pteruchus* are in the British Museum (Natural History) and are referred to by their British Museum registration numbers.

Genus ***PTERUCHUS*** Thomas, 1933 : 232

EMENDED DIAGNOSIS. Microsporophyll borne singly, without subtending organ, on cutinized axis of about same size as rachis. Axis radially symmetrical, cuticle showing similar rectangular cells all over. Microsporophyll, unforked alternate pinnate. Rachis showing lateral wing, and occasional vegetative pinnules, cuticle dorsiventral. Pinnae expanding into rounded or elongate lobed sporangial heads. Heads more or less dome-shaped, non-sporangial surface often rugose. Venation pinnate, shown on sporangial side of heads. This surface completely occupied by pollen sacs: non-sporangial surface covered with cuticle. Pollen sacs borne over

central part of head, but absent over thin margins and lobes and over continuation of pinna on to head. Pollen sacs numerous, more or less cigar-shaped, 0.75 mm. to 2.5 mm. long and 0.75 mm. to 1.5 mm. wide, unilocular, dehiscing by longitudinal slit, wall at maturity consisting of epidermis only, composed of narrow longitudinally elongated uniform cells, sometimes with slightly sinuous outlines. Cuticles of all parts delicate, about  $1\ \mu$  thick, showing faint to pronounced, normally slightly, sinuous cell outlines, and rarely papillae; cells more or less in rows over rachis and pinnae, without apparent orientation over heads. Stomata few, about 5/mm.<sup>2</sup> over heads, exposed or sunken, normally flanked by two lateral and two terminal subsidiary cells, encircling cells normally distinguishable. A few usually tricellular pointed hairs present. Pollen bisaccate, sacci slightly to distinctly offset distally, overlapping or not, on to proximal face of body of grain, longer than wide, as long as or slightly shorter than body, normally more or less parallel sided and ornamented with moderately distinct reticulum, meshes  $2\ \mu$  to  $3.5\ \mu$  wide, walls of mesh about  $1\ \mu$  thick. Body of grain about 50% longer than wide, ends obtuse or bluntly pointed, rarely round, wall between body and sacci normally distinct, body minutely reticulate or almost smooth. Distinct sulcus present, flanked by strip of thicker cutin, about as long as body, not occupying whole space between sacci on distal surface.

Length: 50  $\mu$  (typical).

Total width: 80  $\mu$  (typical).

Ratios (means): Length of body/width of body, 1.27.

Width of whole grain/length of body, 1.54.

Length of body/width of saccus (to distal roots), 1.25.

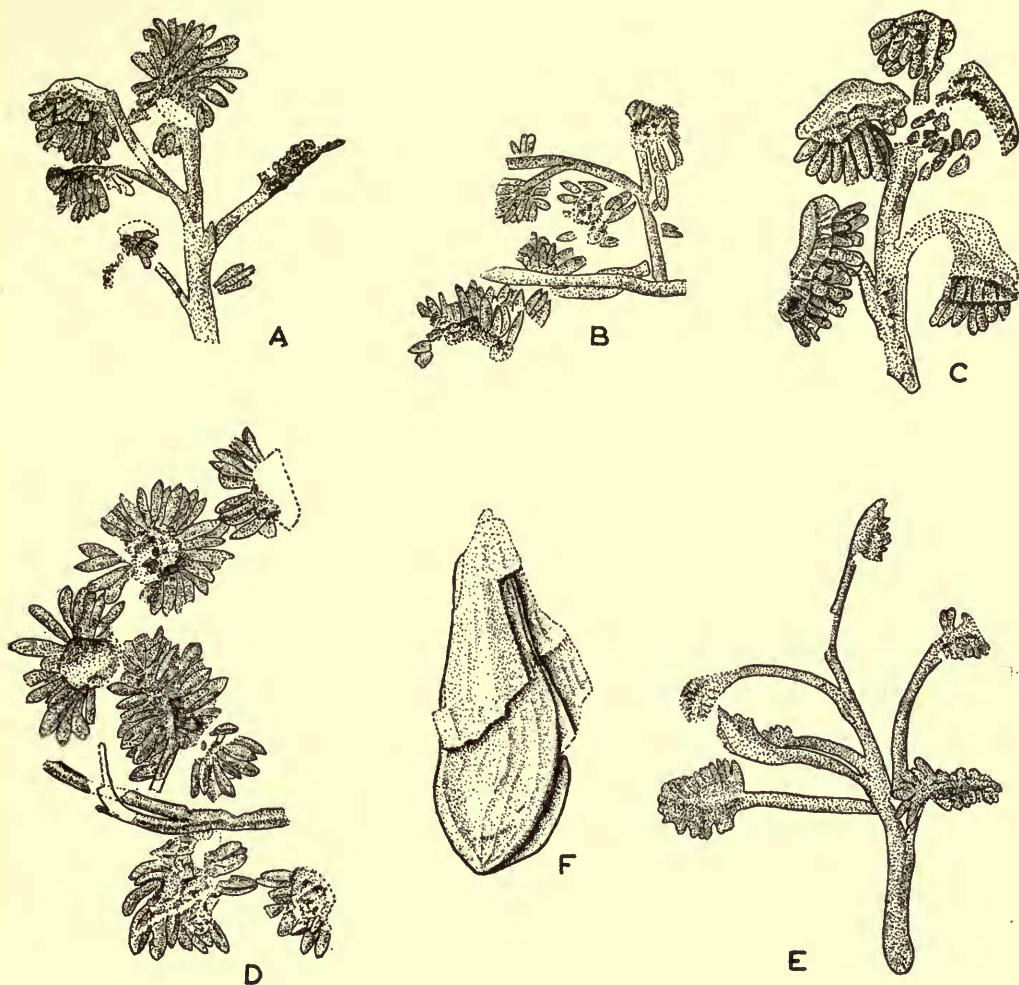
TYPE SPECIES. *Pteruchus africanus* Thomas.

DESCRIPTION. There are two difficulties presented by the Waterfall material. The first is that the specimens split through the fossil, leaving about equal quantities of plant material on both part and counterpart, which are thus mirror-images. This is an important point for it means that the part and counterpart as they stand cannot be superimposed directly, but to see one surface of the organ the part and a transfer of the counterpart must be superimposed (Text-fig. 2A, B). The second is that when macerated, the material, especially if of thick substance, breaks up into small fragments only a millimetre or so square. This is probably because the cuticle is too delicate to hold the coaly substance together when it swells in acid. Hence cuticle data have to be put together from very small pieces, and few stomata, for example, are seen on any one specimen.

The sporophylls are unforked and pinnate, the pinnae being offset towards the upper (adaxial) surface of the rachis (Pl. 24, fig. 4; Text-figs. 2D, 4H). In the small *P. simmondsi*, and the smaller specimens of *P. africanus* this is not obvious, although it can be deduced from the course of the cellular striae of the pinnae, which are interrupted by the lower surface of the rachis, but viewed from the upper surface, continue on to the rachis (Text-figs. 2D, 4H). This feature, together with the pinnate habit, and the lateral wing on the rachis, imparts bilateral symmetry to the organ.

Two specimens of *P. africanus* were still attached to short lengths of axis (Pl. 25, (fig. 2; Text-fig. 1B): one specimen of *P. dubius* is probably similar (Pl. 24, fig. 6)



FIG. 1. *Pteruchus africanus*, *P. dubius*

A-D, *P. africanus*. A, sporophyll with some heads pointing towards the base of the organ, showing rugose non-sporangial surface of heads, a divided pinna, and, in heads with pollen sacs pointing downwards, undisturbed cell rows on the pinnae. V.42684.  $\times 2.5$ . B, two sporophylls, one attached to a piece of the axis (running horizontally) and one detached. V.42688.  $\times 2.5$ . C, sporophyll (*P. peltatus*) showing marginal attachment of pinna in uppermost and lowest right-hand heads. V.23386.  $\times 2.5$ . D, sporophyll attached to a length of axis (running horizontally). V.42685.  $\times 2.5$ .

E, *P. dubius*. Small complete sporophyll showing unforked habit and some divided pinnae. V.42686.  $\times 5$ .

F, *P. africanus*. A pollen sac compressed laterally, showing dehiscence slit. The specimen is partly overlain by another pollen sac.  $\times 25$ .

while one specimen of *P. simmondsi* had bits of cutinized plant matter, possibly of, the axis, sticking to the base of the rachis. The two specimens of *P. africanus*, and probably the specimen of *P. dubius* also, are attached singly, not in a cone or "flower", and either at right angles to the axis, or else curving away from it at a wide angle. Other specimens of all three species showing the sporophyll base often (8 out of 11) show a curvature, suggesting that the sporophyll normally came to lie at a wide angle to the axis.

None of the attached specimens shows any subtending organ on the axis, nor any sign of one such as a scar.

The central part of the axis is raised but the organ does not show strong relief. It does not show a wing (Pl. 25, fig. 2). The cuticle is extremely thin, but shows somewhat obscure outlines of rectangular cells all over, and again, no sign of a wing (cf. p. 313). It was therefore radially symmetrical (at least externally). The fact that the organ is cutinized and of low relief suggests that it had not undergone much secondary thickening, and, a connected point, that lignified tissue was not massive.

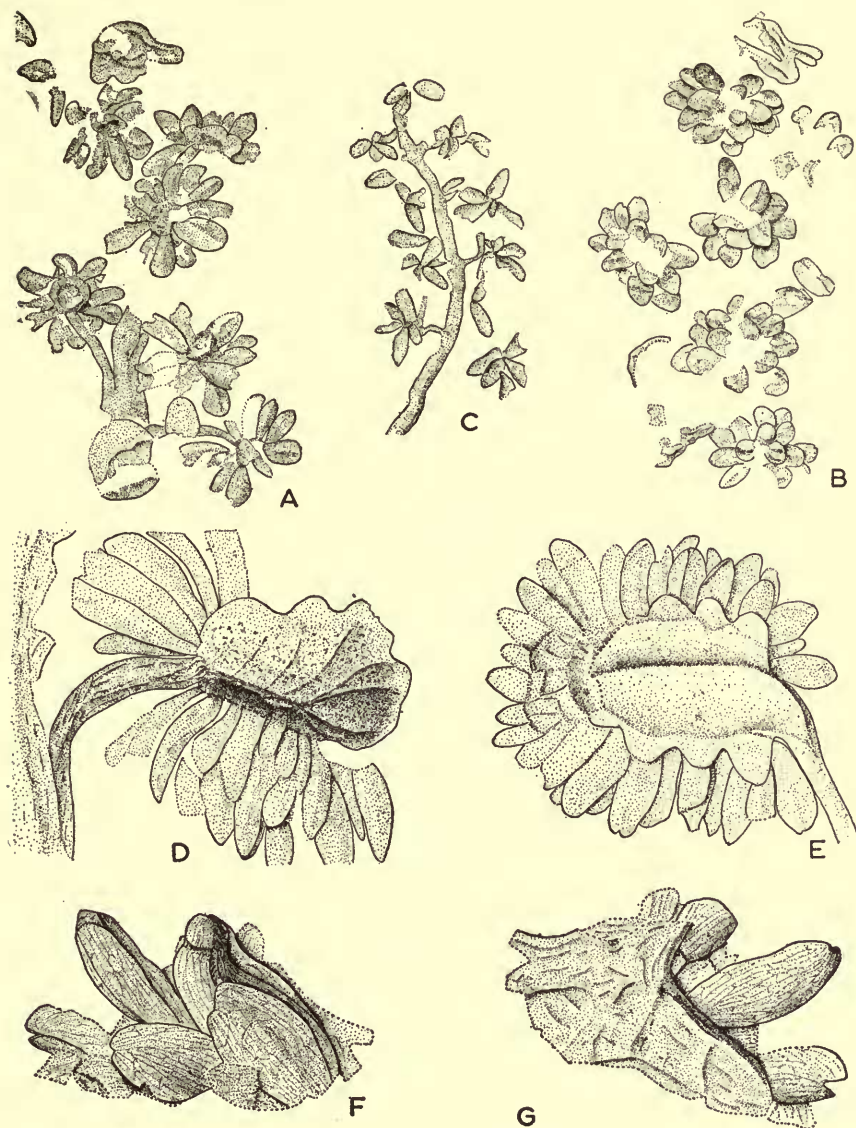
The rachis cuticle is different. It is dorsiventral, showing on the lower surface more or less uniform elongated cells and very few or even no stomata. Similar elongated cells, devoid of stomata, are present over the wing on both surfaces. On the upper surface there is an ill-defined stomatal band, in which the cells are more nearly square, and the stomata are set obliquely, or even at right angles to the rachis long axis (Text-figs. 9B-D, 10B, C). This dorsiventrality is more marked in the larger specimens, though discernible in all.

In all the species the rachis may be raised in irregular lumps, especially in the larger specimens (Pl. 24, figs. 4, 6; Text-figs. 1C, 4H). The lumps leave no trace on the cuticle, and after treatment with acid, stand out as areas of darker matter. They must be wholly internal and are possibly nests of thickened cells.

The pollen sacs almost certainly pointed towards the base of the organ. In some specimens they are so preserved (Pl. 24, fig. 3; Text-fig. 1A, C), and here the cell rows on the pinnæ are not twisted. But in the more numerous specimens in which the heads are rotated in various ways the cell rows are twisted (Text-figs. 2D, 4H).

Vegetative pinnules are rare, they occur in only six of the fifty-one specimens available (*P. africanus* (4), *P. simmondsi* (1), *P. dubius* (1)) and, with two exceptions (V.23360, V.42683) these specimens showed only a single pinnule each. One pinnule of *P. dubius* (V.42683) is set just above the point at which the first pinna (divided in this specimen) arises (Text-fig. 4C). The others lie at varying levels between the sporophyll base and the first pinna. None subtend anything (Pl. 26, fig. 6; Pl. 25, fig. 1; Thomas, 1933, text-fig. 40). In one specimen of *P. africanus* (V.23360), there are two pinnules near the sporophyll base, lying one about 1 mm. above the other (Text-fig. 3B). I cannot find the two minute pinnules figured by Thomas (1933, text-fig. 36) in the specimen called *P. papillatus*, while in the specimen he states showed a basal pair (p. 236) only one is now seen, and there is no clear impression of a second (Pl. 26, fig. 6).

The sporangial heads show the same basic plan, though they differ in proportions and detail (pp. 298, 300, 303). They are attached marginally, though, rather as in a pelargonium leaf, the attachment is mainly on the under (sporangial) side, and may

FIG. 2. *Pteruchus simmondsi*, *P. africanus*

A-C, *P. simmondsi*. A, B, part and transfer of the counterpart of a sporophyll showing swollen base (probably with fragments of axis attached) and, at top, a head compressed laterally, showing smooth non-sporangial surface. V.42687.  $\times 3.75$ . C, small sporophyll showing branching and with (almost certainly) only some of the pollen sacs originally present. V.42691.  $\times 3.75$ .

D-G, *P. africanus*. D, sporangial head showing sporangial surface almost free of pollen sacs, vascular ridges with rows of elongated cells along their crests, area of pollen sac attachment and twisted cell rows on pinna, interpreted as a consequence of rotation of head into the bedding plane. Specimen seen from under (adaxial) surface. Note pinna interrupted by edge or rachis. V.42682.  $\times 7$ . E, sporangial head, seen from non-sporangial surface, showing marginal attachment of pinna and marginal lobes. Surface of head nearly smooth. V.23384.  $\times 7$ . F, G, same fragment, seen from sporangial (F) and non-sporangial (G) sides, showing form of pollen sacs, cell rows on them and their dehiscence slits.  $\times 3.5$ .



be overlapped by the marginal lobes (Pl. 25, fig. 3 ; Pl. 26, fig. 12 ; Text-figs. 2D, 4A, C). Thomas suggested (1933 : 238) that the specimen named *P. peltatus* (V.23386) was peltate. This I believe to have been an error. The specimen is refigured in Text-fig. 1C ; two heads show their marginal attachment, and a transfer shows another was the same ; the others do not show their attachment at all.

*Pteruchus* seems to have been shed as a complete organ, without disarticulating, shedding its pollen sacs, or even all its pollen. There are thus few heads showing their sporangial surface unobscured by pollen sacs. There are eight sporangial heads preserved in this way in *P. africanus*, some incomplete. The sporangial surface is raised in ridges, one ridge more or less opposite each marginal lobe, which coalesce near the point of attachment (Pl. 26, figs. 9, 10 ; Text-figs. 2D, 3C). In two heads, lines of elongated cells were plain, running along the top of these ridges (Text-figs. 2D, 3C) which therefore almost certainly mark the course of the veins. The veins are pinnate, based upon a first division of the main vein near its base into three nearly equal parts, fanning out from the point of attachment (Pl. 26, fig. 10). Over most of the heads, the surface is rough, sometimes raised in little rings about 1 mm. in diameter, but usually showing no distinct pattern. It seems likely that these rings and the rough area in general, mark the insertion of the pollen sacs. It is not clear whether the pollen sacs had any definite arrangement. Usually none is apparent, but in one place (Pl. 26, fig. 9) the rings seem to run in rows parallel with a vein. I can find no evidence that the pollen sacs were borne in groups. Over most of the lobes, around the margins, in areas extending as embayments between the vascular ridges and over the "midrib", i.e. the continuation of the pinna on to the head, the surface is smooth and presumably devoid of pollen sacs (Pl. 26, fig. 10 ; Text-figs. 2D, 3C). Except for a rim, the sporangial surface is uncutinized (Pl. 26, fig. 7) while the number of pollen sacs and the very close-set arrangement of the little rings (where visible) indicate that the pollen sacs were closely packed together, so that there was no epidermal tissue between them.

In the other species the evidence is much less clear. One head of *P. simmondsi* is largely free of pollen sacs, and shows ridges with elongated cells over them, probably set in a pinnate pattern, as in *P. africanus* (Text-fig. 4H), and other heads show that the main vein at least was free of pollen sacs (Pl. 26, fig. 12). I have not seen any heads of *P. dubius* with their sporangial surface unobscured, but several heads show that the main vein at least was free of pollen sacs, as were the marginal lobes (Pl. 25, fig. 3).

Although the evidence is not complete, it is most likely that the heads in all three species were constructed on the same pinnate plan, as indicated by the veins. This is an important point, for it means that the heads were also bilaterally symmetrical and dorsiventral. The heads can thus be described as showing elongated sori over the veins, which become concrescent where the veins join up. I do not know why elongated cells along the vascular ridges are shown in two heads, but not in others. Perhaps the veins became displaced during fossilization.

The non-sporangial surface of the heads is strongly wrinkled in *P. africanus*, slightly so in *P. dubius* and hardly at all in *P. simmondsi*. I believe that some of this wrinkling existed in life (pp. 298, 303), some, however, is almost certainly caused

by the compression of a thick organ. This wrinkling is apt to obscure the cell outlines of the cuticle of the head, especially over the centre of the head, the lobes and margins being, even in *P. africanus*, scarcely wrinkled at all (Pl. 26, fig. 7). As far as can be made out, both cells and stomata lack any preferred orientation, a useful point distinguishing marginal lobe from pollen sac (p. 303 and Text-fig. 10A; Thomas, 1933, text-fig. 48).

The pollen sacs dehisced by a longitudinal slit often (but by no means always) directed towards the centre of the pollen sac group. It also often extends a little way on to the dorsal surface of the pollen sac, so that, in sacs seen dorsal surface uppermost (the majority) it may appear like an apical nick. This has been taken for a terminal pore (Thomas, 1933 : 234), but a transfer reveals its nature, which is confirmed from the cuticle, and also shows a slit down one face (Text-fig. 2F, G). Seen as transparencies, e.g. in transfer, the pollen sac wall is composed of one layer of cells, corresponding to those seen on the cuticle from the pollen sac, and therefore epidermal (Pl. 26, fig. 11; Text-fig. 6D). The periclinal walls as seen in transfer are about 15 times as thick as the cell outlines seen on the cuticle. They may have been thickened. The cells are uniform over the whole pollen sac, except, possibly, next to the dehiscence slit. Here they may be narrower than elsewhere (Text-fig. 6K). However, this appearance may be caused by folding, which is almost invariably seen at this point.

It has been suggested that the pollen sacs were bilocular (Thomas, 1933 : 235), but there is convincing evidence that this is not so. Sections of pollen sacs from each species show only one loculus (Pl. 26, fig. 5), while the wall shows no sign of any partition, unlike a dehisced Angiosperm anther in which the partition between thecae is often visible. I have macerated about 80 pollen sacs, and have never seen more than one pollen mass. On the other hand, it is rather easy to macerate parts of two closely adherent pollen sacs, in which case the appearance described by Thomas could very well arise.

The cuticle of the three species is most variable in every character. In each it varies in thickness from about  $1.5\ \mu$  down to so thin as to be almost impossible to prepare, probably less than  $0.5\ \mu$ . In addition the stomata, even on one specimen, vary in the extent to which they are sunken. In general the most exposed lie on the lower heads or rachis (Text-figs. 8A-K). These two facts strongly suggest that the sporophylls were rather long lived, certainly not ephemeral, and that they varied in response to factors other than genetical, just like leaves for example. This view, however, is contrary to that of Thomas (1933 : 202).

The cell outlines may be faint or plain to see, but in either case are usually decorated with small sinuosities, consisting of projections about  $1\ \mu$  long from the actual outline (i.e. the part occupied in life by the middle lamella) on to the general cuticle surface. In a few specimens of *P. africanus* the cells also bear a papilla (Text-fig. 9D; Thomas, 1933, text-fig. 37). The stomata are based upon the same plan in all three species; that is to say the guard cell poles lie more or less on the general cuticle surface, though in *P. simmondsi* they are sometimes overlapped by the terminal subsidiary cells (Text-fig. 8A), while the aperture is more or less sunken in a depression. The walls of the depression are formed by the lateral subsidiary



cells, which are normally two, but may be divided into three or four. Quite unspecialized encircling cells are usually discernible, but may be absent, especially over the rachis (Text-fig. 9c, d).

The hairs are rare in all three species, scarcely 12 occur in any one specimen but all species show them. On the cuticle the hair base appears as a thickened ring (Text-fig. 6G ; Thomas, 1933, text-fig. 35) the area enclosed by the ring is sometimes

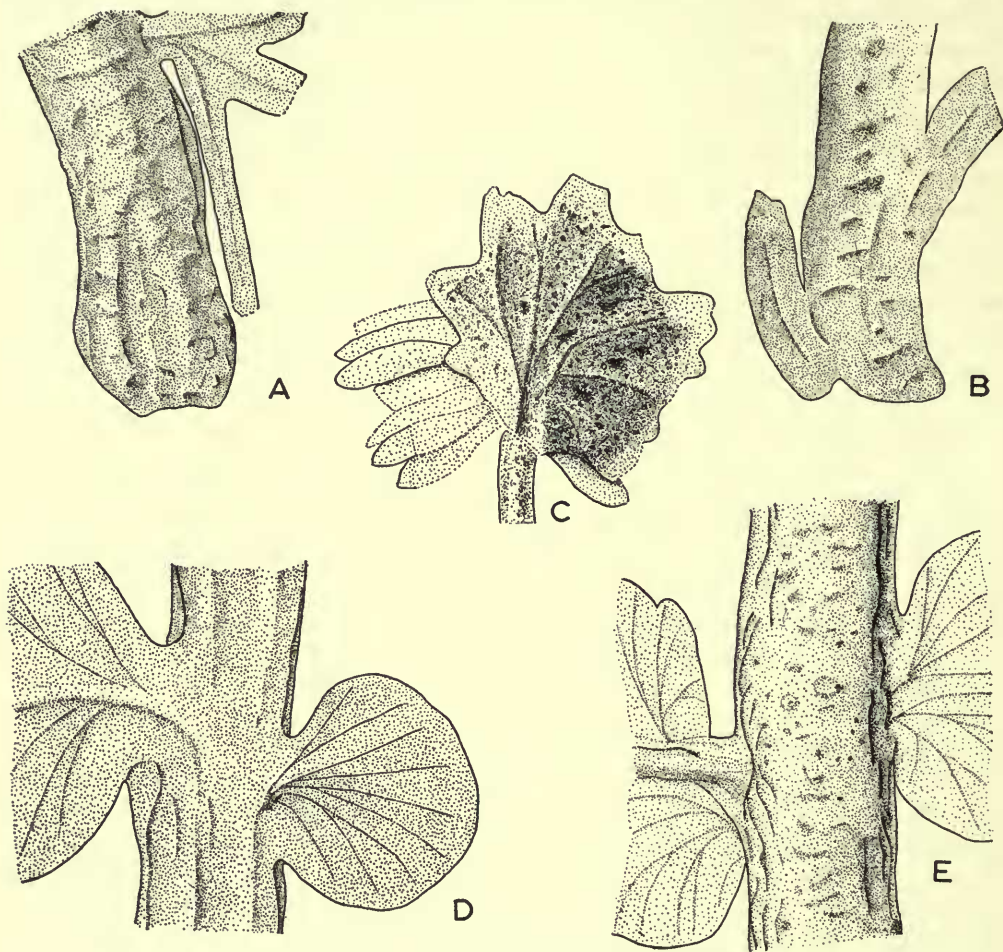


FIG. 3. *Xylopteris elongata*, *Pteruchus africanus*, *Dicroidium feistmanteli*

A, *X. elongata*. A leaf base showing large divided basal pinnule set a short way up from extreme tip of leaf (cf. Pl. 25 ; Text-fig. 5c).  $\times 8$ .

B, c, *P. africanus*. B, sporophyll base (impression only) showing two alternate basal pinnules. V.23360.  $\times 8$ . C, sporangial head, showing sporangial surface free of pollen sacs. It shows main vein, vascular ridges, area of pollen sac attachment, smooth margins and marginal lobes. V.42682.  $\times 8$ .

D, E, *D. feistmanteli*. Equivalent portions of same leaf (E a transfer), drawn from upper (adaxial) (D) and lower (E) surfaces, showing that the pinnae are offset towards upper rachis surface, and venation.  $\times 8$ .



thinly cutinized, sometimes open. On a transfer of the counterpart of a specimen, the hairs themselves may be found. Though often obscure they seem normally to be pointed, and to have three obliquely divided cells, as in Text-fig. 6J. I correlate the hairs with the hair bases on the cuticle, because, though rare, each can be found with regularity, and there is no other structure that I can find to which the hair bases might belong.

It proved difficult to obtain satisfactory pollen preparations of *Pteruchus*. Either the grains stuck together in a mass, obscuring the individuals, or else the pollen sacs were nearly empty, and some of the grains remaining were clearly strays. By breaking up the masses, and examining grains at their edges it was possible to obtain small samples (15 or 20 grains) from every specimen.

The grains are variable (see diagnosis and specific descriptions pp. 298, 300, 303, Pl. 26, figs. 1-4; Text-figs. 10D-G, 11). One of the most prominent features is the sulcus (here the term is confined to the presumed germination furrow lying between the distal roots of the sacchi, and not occupying the whole distal surface of the body of the grain, see Erdtmann, 1947). In many grains the lips touch along their whole length, but in others, otherwise similar, the sulcus gapes open.

### *Pteruchus africanus* Thomas

(Pl. 24, fig. 4, Pl. 25, figs. 1, 2, Pl. 26, figs. 2, 4-11; Text-figs. 1-3, 6-10)

- 1933 *Pteruchus africanus* Thomas, p. 235, pl. 24, figs. 71, 72, text-figs. 34, 35. Fig. of holotype pl. 24, fig. 71.  
 1933 *Pteruchus papillatus* Thomas, p. 237. pl. 24, fig. 77, text-figs. 36, 37. Pollen figd. pl. 24, fig. 77.  
 1933 *Pteruchus peltatus* Thomas, p. 238, text-figs. 38, 39.  
 1933 *Pteruchus hoeigi* Thomas, p. 239, pl. 24 fig. 75, text-figs. 40, 41.  
 1933 *Pteruchus stormbergensis* Thomas, p. 241, text-fig. 43.  
 1933 *Pteruchus* sp. Type X, Thomas, p. 243, text-figs. 47, 48.

Specimens doubtfully identified.

- 1876 *Sphenolepis rhaetica* Geinitz, p. 12, pl. 2, figs. 23, 24.  
 1888 Male flower of *Baiera tenuifolia* Johnston, pl. 27, figs. 2D, E.  
 1890 *Trichopitys johnstoni* Feistmantel, p. 113, pl. 10, fig. 5. Johnston's specimen refigured.  
 1898 *Stachyopitys annularioides* Shirley, p. 13, pl. 18, fig. 1.  
 1917 *Stachyopitys annularioides* Shirley: Walkom, p. 13, pl. 4, fig. 6.  
 1925 Male flower of *Baiera tenuifolia* Johnston: Walkom, p. 85, text-figs. 15, 16. Johnston's Tasmanian material refigured.  
 1933 *Pteruchus annularioides* (Shirley) Thomas, p. 233. New name only.  
 1933 *Pteruchus minor* Thomas, p. 242, text-fig. 46. Small specimen regarded as indeterminable.  
 1933 *Pteruchus* sp. Type Y, Thomas, p. 243. No figure.  
 1947 *Pteruchus annularioides* (Shirley) Jones & Jersey, p. 55, text-fig. 38.  
 1947 *Pteruchus* sp. Jones & Jersey, p. 56. No figures.

Specimen regarded as distinct:

- 1947 *Pteruchus* cf. *africanus* Thomas: Jones & Jersey, p. 55, text-fig. 51.

HOLOTYPE. Brit. Mus. (N.H.) No. V.23384.

MATERIAL. H. Hamshaw Thomas Colln., Brit. Mus. (N.H.) Nos. V.23360, V.23384-88, V.23390-94. J. A. Townrow Colln., Nos. V.42682, V.42684-85, V.42688-90, V.42797.

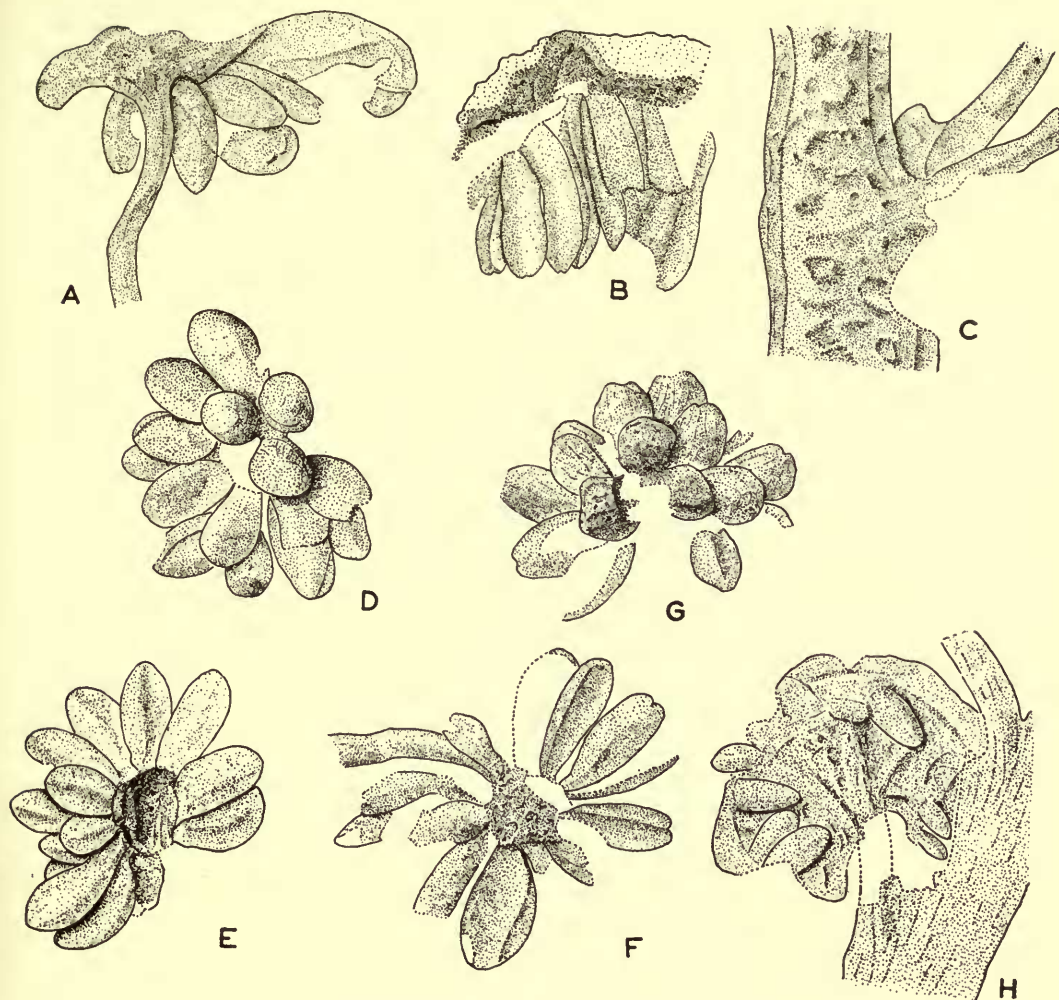
EMENDED DIAGNOSIS. Microsporophyll about 2 cm. long, rachis about 1.5 mm. wide at base. About eight (6-9) long, normally unbranched pinnae present. Heads round to about four times as long as wide, width about 5 mm.; non-sporangial surface strongly rugose, about 10 lobes per head, lobes small in proportion to size of head. Pollen sacs more than 30 per head, about 2.5 mm. long and 1.5 mm. wide. Cell outlines faint,  $1\ \mu$  wide or less, sinuities small, sometimes absent, about  $1\ \mu$  long, usually obtuse, not pointed. Stomata somewhat sunken, poles exposed, pit not overlapped by cutin flanges. Pollen with sacchi scarcely extending on to proximal surface of grain, usually shorter than body of grain, often slightly inflated. Body of grain sometimes bluntly pointed, reticulum on sacchi normally conspicuous, meshes about  $3\ \mu$  in diameter, walls about  $1\ \mu$  thick; ornamentation on body faint or absent. Dimensions in  $\mu$  (standard deviations bracketed): Length of body 46.25 (6.45); width of body 32.2 (7.45); length of sacchi 35.2 (12.6); width of sacchi 36.2 (9.2); height of grain 20 (2.8); total width of grain 63 (6.3).

DESCRIPTION AND REMARKS. The pinnae are almost always unforked, but in two specimens (V.42684, V.42707, Text-fig. 1A) certain pinnae branch on leaving the rachis. When compressed laterally (Text-fig. 1A) the heads appear dome-shaped and the non-sporangial surface is raised in irregular lumps. Probably, therefore, the wrinkling of the cuticle of the heads is not all connected with the compression of a thick organ, but is partly original. The pollen sacs, while varying considerably in size and form, are normally not much inflated (Pl. 24, fig. 4; Text-fig. 2F, G).

Cell outlines are sometimes so faint that they are scarcely visible and, about one-third of the preparations lack them altogether. When present the sinuities are small ( $1\ \mu$  or less) and grade gradually into the residue of the cuticle so that it is difficult to decide exactly where they end. (Text-fig. 7A). Text-fig. 8B, C show two stomata from the same specimen. One, Text-fig. 7B, comes from an upper head, the other, Text-fig. 8C from a lower head. Each is typical of the degree of sinking seen on upper and lower heads respectively. Stomata from a lower head, but sunken like Text-fig. 8B, or stomata from an upper head but nearly exposed like Text-fig. 8C number less than 1 in 6. Almost exposed stomata (Text-fig. 10) number about 1 in 5 on the marginal lobes of some lower heads.

In most pollen grains the insertion of the sacchi is similar to that shown in Pl. 26, fig. 2, they do not extend on to the proximal surface of the body of the grain, but this character is a variable one, and some grains show overlap on to the proximal surface (Text-fig. 10F). As seen in tangential longitudinal view, the body of the grain is usually about as broad as high (Pl. 26, fig. 2; Text-fig. 10F, G). The reticulum on the sacchi is normally prominent, but on the body, faint, and sometimes absent, at least from the proximal surface where this is seen in optical section. (Text-fig. 10F, G). All the various alternatives mentioned above can often be found within a preparation made from a single pollen sac, so that there is no question that the sundry variations in pollen form among the specimens determined as *P. africanus* indicate that more than one species of microsporophyll is present.

All but three of the specimens given separate specific names by Dr. Hamshaw Thomas are here merged with *P. africanus*. They form a series which cannot be split. As regards gross form, Dr. Thomas' specimens vary, but when my material

FIG. 4. *Pteruchus simmondsi*, *P. dubius*

A, *P. simmondsi*. Part of a sporangial head showing marginal attachment of pinna. V.42692.  $\times 15$ .

B, C, *P. dubius*. B, part of a head showing slightly rugose non-sporangial surface and form of pollen sacs. V.42683.  $\times 10$ . C, lowest (divided) pinna of a sporophyll, showing a pinnule set just above insertion of pinna, drawn from under side of specimen. V.42683.  $\times 10$ .

D-H, *P. simmondsi*. D, E, same sporangial head before (D) and after (E) transfer, showing shape and spreading habit of pollen sacs. No marginal lobes seen. V.42693.  $\times 10$ . F, G, the part (F) and transfer of counterpart (G) of a sporangial head, showing nearly smooth non-sporangial surface of head (F) and three marginal lobes (G). A fourth marginal lobe broke off in preparation. V.42687.  $\times 10$ . H, sporangial head seen from sporangial surface; whole specimen seen from upper surface. It shows marginal lobes, pollen sacs vascular ridges and pinnae from this side, not interrupted by edge of rachis (cf. Fig. 2D). V.42681.  $\times 10$ .



is added to his, the new specimens do not fall into his species, but fill in the gaps between them (and, indeed, extend the variation) so that the whole material forms one continuously varying series. Thomas noted the dorsiventrality of the rachis cuticle, but did not state in his cuticle figures which surface is drawn. Text-fig. 9A-D shows the cuticle from a single specimen (V.42682), it comprises very nearly all the variation seen in Thomas' figures. As already noted, the pollen points away from the suggestion that more than one species is involved. I conclude there is only one species, which is compared with the other two here recognized on p. 307, Table I.

The specimens named *Pteruchus annularioides* (pp. 297, 310) from Queensland are only doubtfully identified with *P. africanus*. The holotype is an impression only, and shows little detail (Jones & Jersey, 1947 : 55). From the existing descriptions and figures it is impossible to identify, or to reject, this species with regard to any of the better known species of *Pteruchus*. However, the figured specimens resemble small specimens of *P. africanus*, and agree in dimensions. It may be that these specimens, like the Waterfall material, are split in such a way that not all the pollen sacs are visible on any one specimen (Text-fig. 2c). Re examination of the holotype might well show that *P. annularioides* and *P. africanus* are identical ; and if so Shirley's name will have priority. While this is uncertain, however, the name *P. africanus* is provisionally retained.

The earlier records of Geinitz (1876)a and Feistmantel (1890) likewise cannot be identified, or excluded at present. When these specimens are re-examined the question of prior names will again arise. The records of Johnston (1888) and Walkom (1925) do not affect the nomenclature, since they did not give a particular name to the specimens now considered ; the leaf *Czekanowskia* (originally *Baiera*) *tenuifolia* (Johnston) Jones & Jersey (1947) is now believed to have nothing to do with *Pteruchus* (see p. 310).

### *Pteruchus dubius* Thomas

(Pl. 24, figs. 5, 6 ; Pl. 25, fig. 3 ; Pl. 26, fig. 1 ;  
Text-figs. 1E ; 4B, C ; 7B ; 8D ; 10A-C ; 11A, B)

- 1933 *Pteruchus dubius* Thomas, p. 241, text-figs 44, 45. Single head and part of pinna. Holotype, text-fig. 44.  
1942 *Pterorrachis barrealensis* Frenguelli, p. 311, pl. 2. Large specimen, impression only.  
1944 *Zuberia zuberi* Frenguelli, p. 16, pl. 2, text-fig. 12. Same specimen described. Text-fig. 12 reconstruction.  
1947 *Pteruchus* cf. *africanus* Thomas : Jones & Jersey, p. 55, text-fig. 51. Impression only.

HOLOTYPE. Brit. Mus. (N.H.) No. V.23389.

MATERIAL. J. A. Townrow Colln., Nos. V.42683, V.42686, V.42695.

EMENDED DIAGNOSIS. Microsporophyll about 4 cm. long, rachis about 2.5 mm. wide at the base. About four (3-6) long, slender, often branched pinnae present. Heads elongated, from three to five times long as broad, width about 4 mm., non-sporangial surface slightly rugose, head bearing about 15 marginal lobes. Lobes small in proportion to head. Pollen sacs about 100 per head, about 2 mm. long and 1.25 mm. wide. Cell outlines faint, 1  $\mu$  wide or less, sinuities small, normally

present,  $1\ \mu$  to  $1.5\ \mu$  long, normally slightly pointed. Stomata more or less exposed, lateral subsidiary cells often thickened over their whole cutinized surface. Pollen with sacci normally extending on to proximal surface of grain, as long as body of grain, usually parallel-sided. Reticulum on sacci normally conspicuous, meshes about  $2\ \mu$  in diameter, walls about  $1\ \mu$  thick, body smooth or very nearly so. Dimensions in  $\mu$  (standard deviation bracketed): Length of body  $53.0$  ( $7.35$ ); width of body  $43.3$  ( $6.2$ ); length of sacci  $53.0$  ( $7.05$ ); width of sacci  $33.1$  ( $6.85$ ); height of grain  $50.0$  ( $4.95$ ); total width of grain  $88.3$  ( $15.3$ ).

DESCRIPTION AND REMARKS. The material includes two complete sporophylls (V.42683 V.42686; Pl. 24, fig. 5, Text-fig. 1E). Both are unforked. This species, like the others is simple and not forked. About half the pinnae are divided. In some cases this can be seen (Pl. 24, fig. 6; Text-figs. 1E, 4C and Frenguelli, 1942, pl. 2), in other cases there are more sporangial heads than pinna origins, so a division is deduced. Compressed laterally the heads are of thick substance (Pl. 24, fig. 5) and of slightly rugose surface, but much less so than in *P. africanus*. The pollen sacs are almost cylindrical, and on two small heads I counted over 100, so that this figure given in the diagnosis is probably on the conservative side; they are so crowded, however, that counting is difficult.

The cell outlines are apt to be faint, but they almost always show sinuosities. The sinuosities are larger than in the other two species (about  $1.5\ \mu$ ). The central part of the outlines is thin, and the sinuosities at their ends grade into the generality of the cuticle, but are distinct elsewhere, (Text-fig. 7B). The stoma in Text-fig. 8D is from a head at the top of the specimen (V.42683) where it is typical. A few, probably less than 1 in 10, are more sunken, but none so sunken as the stoma shown in Text-fig. 8B. On the lower heads the stomata may be even more exposed (Text-fig. 10). In about half the stomata seen the lateral subsidiary cells are thickened uniformly. On staining this shows as a darker area but without staining it is not visible (Text-figs. 8D, 10; Thomas, 1933, text-fig. 45).

The pollen is shown in Pl. 26, fig. 1 and Text-fig. 11A, B. The sacci overlap the proximal surface of the grain, so that they lie very nearly in the *para* position, while the body of the grain, seen in tangential longitudinal view, is higher than wide. The ornament on the sacci is usually prominent, but on the body none or almost none is visible, the proximal surface, when seen in optical section, showing at most a minutely scabrid surface. As in *P. africanus* all variants can be found in a preparation from one pollen sac.

The holotype consists of a single head, and part of a pinna. It is split through, leaving about equal proportions of plant material on both part and counterpart. Each shows part of the head and some of the pollen sacs, both of which correspond in their form with the other material here identified with *P. dubius*. However, if the part and counterpart are superimposed as they stand, because of the way the specimen is split, the pollen sacs appear to have originated all round the head (Thomas, 1933 : 242, text-fig. 4I). The pollen and cuticle are normal. For these reasons, I identify my material with Dr. Thomas' specimen.

The single large specimen described and figured by Frenguelli (1942, 1944) is an impression only, and there is no counterpart. Judging from the figures the specimen

comprises the basal three-quarters, approximately, of the sporophyll, and there is no evidence whatever that it was forked. It is a larger specimen than any other so far discovered, but agrees with the present material in general appearance and in structure, but no cuticle or pollen is available. The specimen is therefore identified with *P. dubius*, and is included above in the synonymy of that species. I agree with Frenguelli (1942) that the other two species placed in *Pterorrachis* probably



FIG. 5. *Dicroidium odontopteroides*, *Xylopteris elongata*

A, *D. odontopteroides*. Leaf, seen from under side, showing curving leaf base and rotated pinnae.  $\times 1$ .

B, C, *X. elongata*. B, small leaf showing a small undivided basal pinnule (see also Pl. 25).  $\times 1$ . C, lower portion of large leaf showing larger, divided, basal pinnule (see also Fig. 3A).  $\times 1$ .

belong to different plants. The ascription of *P. dubius* to the leaf called *Zuberia zuberi* is discussed below (p. 313).

Frenguelli (1944, text-fig. 12) gives a reconstruction based on his specimen. My interpretation of the material is very different from his, and I regard his figure as misleading in most respects.

The specimen of *Pteruchus* cf. *africanus* described by Jones & Jersey (1947) is an impression, and as they remark, scarcely identifiable. However, it has divided pinnae, considerably elongated heads and small pollen sacs, and is therefore more likely to be a specimen of *P. dubius* than *P. africanus*, with which they tentatively compared it.



*Pteruchus simmondsi* (Shirley) Thomas

(Pl. 24, figs. 1-3; Pl. 26, figs. 3, 12; Text-figs. 2, 4, 6-8, 11)

- 1898 *Stachyopitys simmondsi* Shirley, p. 13, pl. 18, fig. 2. Diagnosis and fig. of holotype, but without detail. From Denmark Hill, Ipswich, Queensland. Ipswich Series.  
1917 *Stachyopitys simmondsi* Shirley: Walkom, p. 13. Shirley's material, no figure.  
1933 *Pteruchus simmondsi* (Shirley) Thomas, p. 233. New name only.  
1944 *Stachyopitys anthoides* Frenguelli, p. 365, pls. 1, 2; text-fig. 1. Pl. I, fig. 3, distinct. Several specimens from Argentina.  
1947 *Pteruchus simmondsi* (Shirley): Jones & Jersey, p. 55, Shirley's material discussed. No figure.

EMENDED DIAGNOSIS. Microsporophyll about 1.5 cm. long, rachis with bulbous base. Width just above base about 1.5 mm. About 8 (4-11) short unbranched pinnae. Heads round, width from lobe to lobe about 2.5 mm.; non-sporangial surface almost or quite smooth, substance thin, 4 (3-5) lobes per head, lobes large in proportion to head. Pollen sacs, about 15 per head, about 1.5 mm. long and 1 mm. wide. Cell outlines usually distinct, about 1.5  $\mu$  wide, straight or with small obtuse sinuosities less than 1  $\mu$  long. Stomata sunken, poles sometimes covered by terminal subsidiary cells, pit sometimes overhung by cutin flanges on lateral subsidiary cells. Pollen with sacchi extending on to proximal surface of grain, parallel-sided or tapering. Reticulum on sacchi conspicuous, meshes about 5  $\mu$  in diameter, walls about 1.5  $\mu$  thick; ornament on body usually conspicuous. Dimensions in  $\mu$  (standard deviations bracketed): Length of body 58.0 (6.1); width of body 47.5 (4.25); length of sacchi 55.5 (6.5); width of sacchi 34.0 (4.05); height of grain 42.25 (4.35); total width of grain 84.5 (12.6).

HOLOTYPE. Queensland Geological Survey Colln., No. F256.

MATERIAL. J. A. Townrow Colln., Brit. Mus. (N.H.) Nos. V.42681, V.42687, V.42691-94.

DESCRIPTION AND REMARKS. The pinnae are short, compared with the size of the whole organ and no branching ones were seen; they are alternate, but may be almost opposite (Pl. 24, fig. 3, Text-fig. 2A-C). The bulbous base is seen in the holotype (Pl. 24, fig. 2) and in two specimens from the Waterfall (Text-fig. 2A).

The marginal lobes are seldom seen complete. They may look like pollen sacs, but can be distinguished on the cuticle (p. 295). It seems that, when ripe, the pollen sacs drew away from each other, so that both they and the marginal lobes came to lie almost back to back (Text-fig. 4F). Thus in a transfer there is very little tissue of the lobes which can stick on to the balsam. Some, however, are seen in Text-fig. 4F, and others laterally compressed in Text-fig. 2A. They are large in proportion to the head, so that the whole head, when flat, has an appearance somewhat resembling a trefoil (Pl. 26, fig. 12). The head compressed laterally shows that its substance was thin and the non-sporangial surface almost or quite smooth. The pollen sacs are short and much inflated, sometimes almost globose (Text-fig. 4D).

Although the cuticle is little if any thicker than in the other species, the cell outlines are both thicker and more distinct. The small sinuosities are sharply marked off from the rest of the cuticle, being less than 1  $\mu$  long but about 2  $\mu$  wide

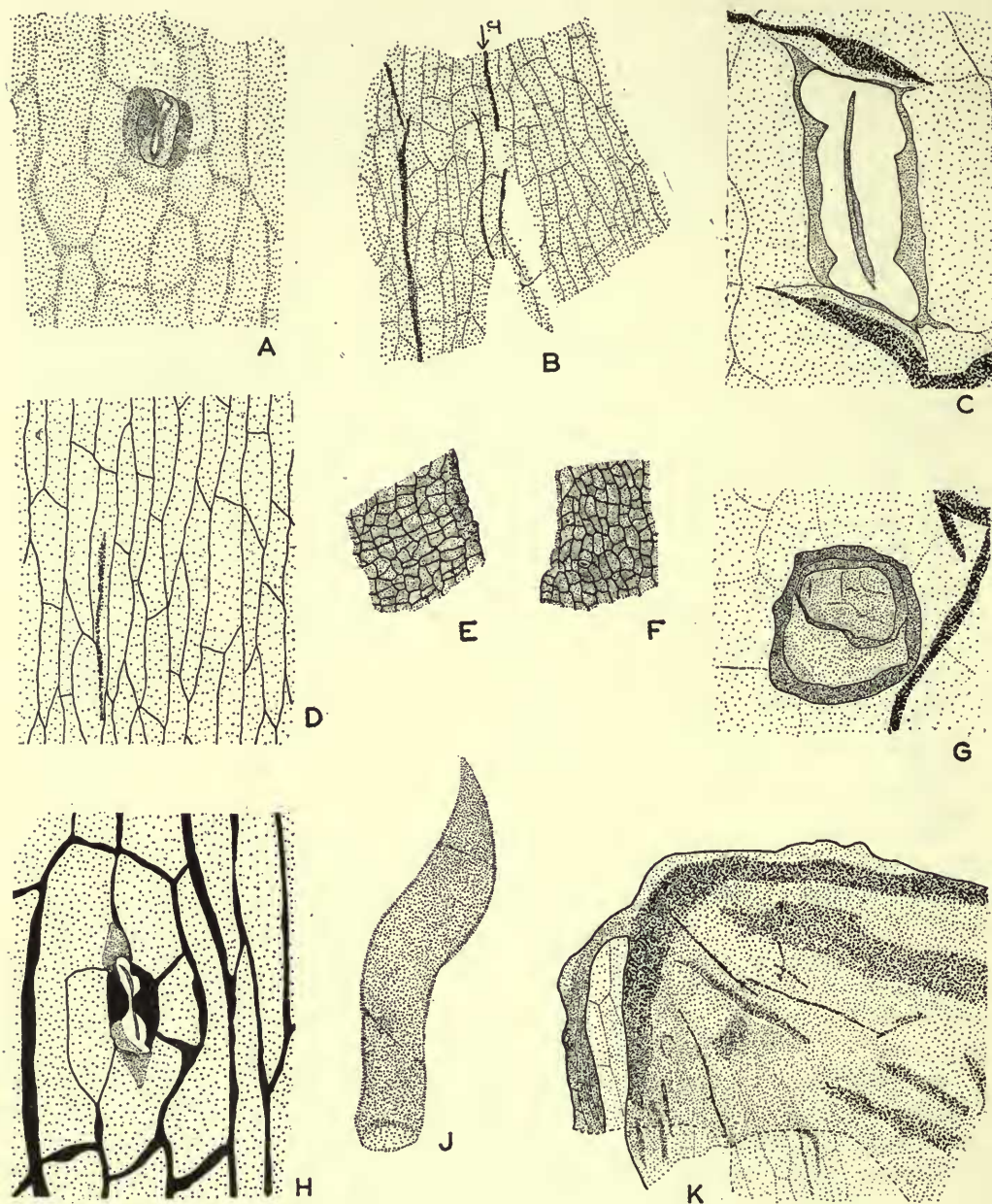


FIG. 6. A, *Phoenicopsis elongatus* ; B-D, G, *Pteruchus africanus* ; E, F, *Xylopteris elongata* ; H, *Czekanowskia tenuifolia* ; J, K, *P. simmondsi*

A, fragment from thinner cuticle (? lower) and a stoma.  $\times 416$ . B, cuticle from axis, showing more or less uniform cells all over. (J) marks position where two surfaces join. V.42688.  $\times 94$ . C, abnormally exposed stoma from a marginal lobe of head near base

at the base the central part of the outline is wide, and with obscure edges (Text-fig. 7D). The stomata are nearly always sunken, nearly exposed ones (such as in Text-fig. 7C), probably number about 1 in 10. Text-figs. 8A, H show stomata with covered guard cell poles, and cutin flanges on the subsidiary cells. Both sorts together make up about 75% of all those seen.

The pollen is shown in Pl. 26, fig. 3 and Text-fig. 11C, D. The sacchi normally overlap on to the proximal surface of the grain, but do not always, and the body of the grain in tangential longitudinal view is commonly wider than high. On the body some ornament is usually visible, sometimes a reticulum, more often irregular lines of thicker cuticle.

Thanks to the kindness of Dr. O. A. Jones, University of Queensland and of the Director, Queensland Geological Survey, to both of whom I am much indebted, I have been able to examine the holotype of *P. simmondsi* here refigured (Pl. 25, fig. 2). The specimen is an impression only, but it is identified with *P. simmondsi* because it agrees in dimensions with the present material, and because it shows the bulbous base, delicate, short pinnae and inflated pollen sacs (probably dehiscent in the holotype) characteristic of this species. The impressions of the cellular outlines are very faintly seen on some of the pollen sacs; they agree in shape and dimensions with those seen on cuticle. There are two difficulties: the pollen sacs are few, but I suspect this is connected with the way the specimen has split (cf. Text-figs. 2A-C), and one pinna on the holotype may be divided. I cannot decide whether it is, or whether we are looking at part of the sporangial head.

Frenguelli's (1944a) record consists of several well-preserved specimens. He does not give detail in his description, but the form and size of his specimens agree closely with mine, and so I identify his material with *P. simmondsi*; which name therefore takes priority. The specimen figured in his pl. 1, fig. 3 shows a number of pollen sacs attached to a somewhat elongated head; it is therefore distinct from *P. simmondsi*. It may be a small specimen of *P. africanus*, but there is not enough information for an identification.

#### GENERAL DISCUSSION

##### (1) *The Species of Pteruchus*

The three species (*P. africanus*, *P. dubius* and *P. simmondsi*) are usually distinguished readily (see Table I), but fragments may be difficult to classify, and in some species one or other character is poorly developed, and rather as in another species. The specimen originally described as *Pteruchus edwardsi* Thomas is here transferred to *Stachyopitys*.

of a sporophyll. V.42689.  $\times 975$ . D, cells from cuticle of pollen sac (cf. Pl. 26). V.42690.  $\times 250$ . E, F, cuticle from opposite sides of axis, originally joined along their adjacent edges, showing more or less uniform cells all over and one stoma. From specimen figured Pl. 25.  $\times 50$ . G, trichome base. V.42689.  $\times 975$ . H, fragment from leaf surface with thicker cuticle (? upper) with a stoma.  $\times 416$ . J, trichome from the transfer of a counterpart. V.42687.  $\times 310$ . K, cuticle from apex of a pollen sac showing dehiscence slit, and in places, the cell outlines. V.42694.  $\times 94$ .



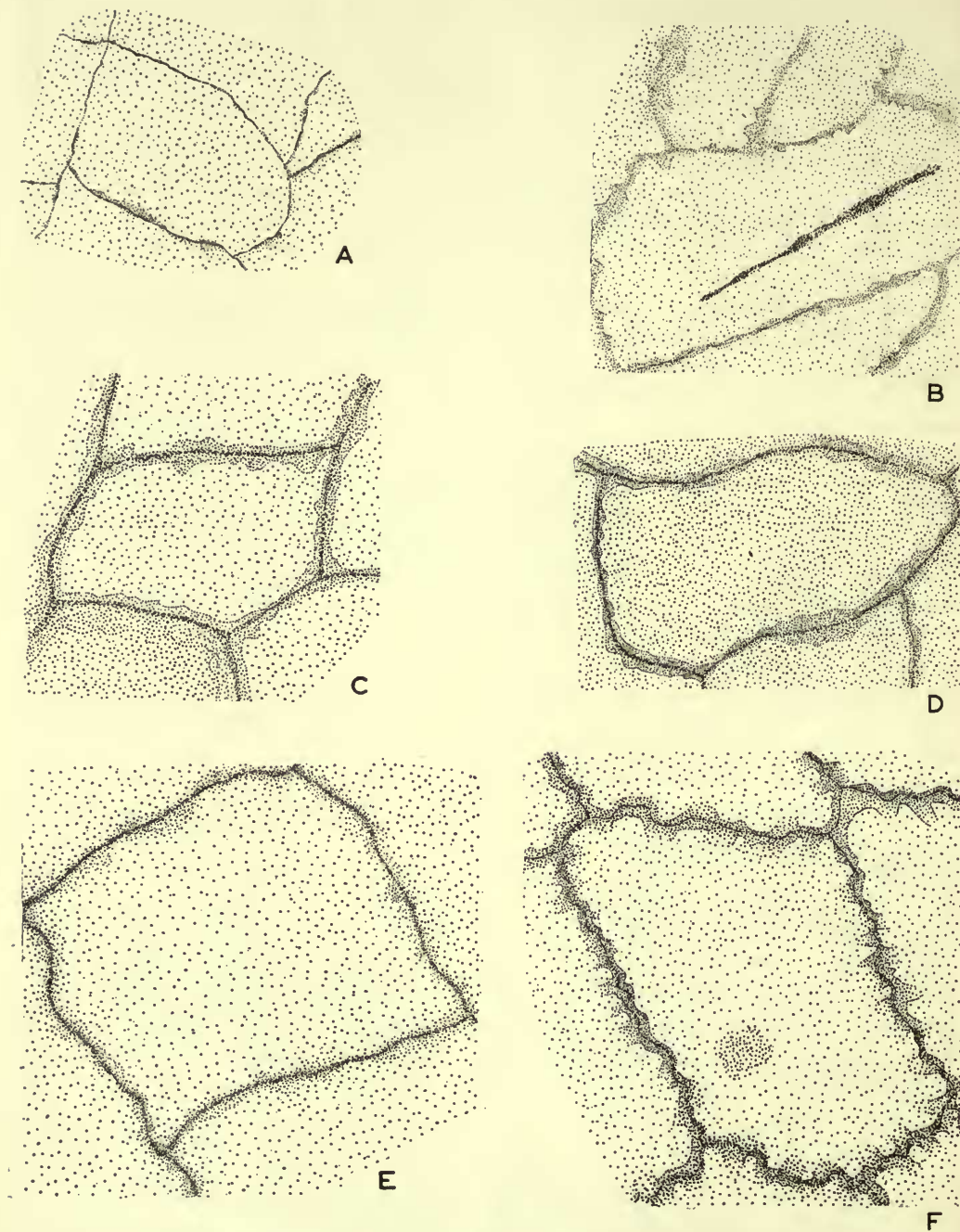


FIG. 7. A, *Pteruchus africanus*; B, *P. dubius*; C, *Xylopteris elongata*; D, *P. simmondsi*; E, *Dicroidium odontopteroides*; F, *D. feistmanteli*

Portions of cuticle from non-sporangial surface of sporangial heads, or lower surface of lamina of leaves, showing form of cell outlines. All  $\times 975$ .

*Stachyopitys edwardsi* (Thomas) nov. comb.

1933 *Pteruchus edwardsi* Thomas, p. 240, pl. 24, fig. 74, text-fig. 42.

I have examined the holotype (the only specimen) which is preserved as a hollow cast. It does not show much detail and lacks cuticle or pollen. I agree with Dr. Thomas that the branching is spiral, and the heads peltate with a single ring of about 8 marginal sporangia. The specimen thus differs widely from *Pteruchus* as here defined.

It bears some resemblance to *Stachyopitys preslii* Schenk (1867 : 185, pl. 64, figs. 9-12), the type species, and this genus is probably its best resting place at present (see also Seward, 1903 : 66, 67, pl. 9, fig. 2 and Gothan 1914 : 62, 63, pl. 29, fig. 4 pl. 33, fig. 3).

TABLE I.—*Comparison of the Species of Pteruchus*

Character	Species		
	<i>P. africanus</i>	<i>P. dubius</i>	<i>P. simmondsi</i>
Length . . .	2.5 cm. approx.	4 cm. approx.	1.5 cm. approx.
Pinnae . . .	About 5 mm. long, rarely divided	About 1 cm. long, often divided	About 3 mm. long, not divided.
Sporangial heads	Elongated to round, of thick substance, strongly rugose, <i>ca.</i> 10 lobes per head	Elongated, of thick substance, slightly rugose, <i>ca.</i> 15 lobes per head	Iso diametric, thin substance, smooth or nearly so, 3-5 lobes per head.
Pollen sacs . . .	More than 30 per head, about 2.5 mm. long, about twice as long as wide, slightly inflated	100 or more per head, about 2.0 mm. long, about twice as long as wide, not, or scarcely inflated	Approx. 20 per head, about 1.5 mm. long, less than twice as long as wide, markedly inflated.
Cell outlines . . .	Faint, about 1 $\mu$ wide, straight or slightly sinuous, sinuosities obtuse	Faint, about 1 $\mu$ wide, normally sinuous, sinuosities normally slightly pointed	Distinct, 1-2 $\mu$ wide, straight or slightly sinuous, sinuosities obtuse.
Stomata . . .	Normally somewhat sunken, poles of guard cells exposed, pit not overhung	Normally exposed or slightly sunken	Normally strongly sunken, poles of guard cells sometimes covered, pit sometimes overhung by cutin flanges.
Pollen :			
(a) Size . . .	Length <i>ca.</i> 46 $\mu$ : Total width <i>ca.</i> 63 $\mu$	Length <i>ca.</i> 53 $\mu$ : Total width <i>ca.</i> 88 $\mu$	Length <i>ca.</i> 58 $\mu$ : Total width 84.5 $\mu$ .
(b) Insertion of sacchi	Not or scarcely overlapping on to proximal surface, body high as wide	Overlapping on to proximal surface, body higher than wide	Overlapping on to proximal surface, body wider than high.
(c) Ornament . . .	Obscure on body, meshes on sacchi about 3 $\mu$ diameter	Body smooth or nearly so, meshes on sacchi about 2 $\mu$ in diameter	Body with fairly distinct reticulate ornament, meshes on sacchi about 5 $\mu$ in diameter.

(2) *The Ascription of Pteruchus to Leaves of the Dicroidium-Xylopteris Group.*  
 (a) *Ascription of the Genus Pteruchus*

Thomas (1933) suggested that *Pteruchus* was the pollen organ of the leaves here called the *Dicroidium-Xylopteris* group, on account of a general similarity in cuticle, and association at the Waterfall and at one or two other localities, e.g. Denmark Hill, Ipswich, Queensland. I most fully agree. A much stronger case can now be made out than that which Dr. Thomas was able to advance.

The *Dicroidium-Xylopteris* group (see p. 288) consists of 12 or 14 extremely similar species of leaf. It is not clear whether they are best dealt with under two genera, as they are at present, or merged in one, *Dicroidium* having priority. The forking habit is common to all whilst their cuticles offer no basis for separation into different genera. It may be best to make some arbitrary separation, perhaps on the number of veins at a given point in the leaf segment, but no workable distinction on such lines is yet apparent (see Jones & Jersey, 1947 : 30 for *X. tripinnata* and Townrow, 1957 : 43-45 for *D. superbum*).

Evidence for the reference of the genus *Pteruchus* to these leaves comes from agreement in anatomical structure, and from association.

(1) *Agreement in Structure*

Both leaves and microsporophylls are borne in the same way on axes that are similar, though of different sizes (p. 290, Pl. 25, figs. 2, 5). The venation of the heads of *P. africanus* at least is built upon a first division, very near the point of attachment, into three more or less equal branch veins. This is just like the venation of *Dicroidium odontopteroides*, and sometimes of *D. feistmanteli* and *D. coriacium* (Pl. 26, fig. 10 ; Text-fig. 3D, E ; Townrow, 1957 : 34, 35, text-figs 4, 9D). The cuticles of the rachises of both leaves and microsporophylls are very similar. Both show a lateral wing, both are dorsiventral by reason of the same cellular pattern, and the distribution of stomata is the same (Text-fig. 9A-D ; Townrow, 1957 : 26, text-fig. 2). As regards detailed cuticle structure, the stomata are built on exactly the same plan in both leaf and microsporophyll, being distinguishable only because the stomata of *Pteruchus* are usually smaller than on the leaves (Text-fig. 8), while both also show occasional tricellular pointed hairs of identical form (Text-fig. 6J). Other points of agreement are in the construction of the sinuosity of the cell outlines (Text-fig. 7) and in the presence of papillae (rare in *Pteruchus*) (Text-fig. 9D ; Townrow, 1957, text-figs. 5, 6).

(2) *Evidence from Association*

The genus *Pteruchus* has now been found in twelve localities, one at the Waterfall, Natal, ten in the Ipswich Series, Queensland, and one, near Ischigualasto Argentina. The position, however, is not entirely straightforward. Some of the associated leaves at the Waterfall have not yet been identified ; in the Ipswich Series (Jones & Jersey, 1947) the specimens are nearly all impressions, and only two are figured, so that there is inevitably some doubt as to the identifications ; while at Ischigualasto the complete species list is not given. For the present purpose the Ischigualasto locality is ignored (but see p. 313), all records of *Pteruchus* are treated simply as



records of the genus (the species are discussed later, p. 312) and some of the most critical leaves are lumped into groups. So far as I can judge, none of these steps alters the conclusions which may be drawn.

At the Waterfall, *Pteruchus* is quite a common fossil, represented in the Townrow Collection by 51 specimens (*P. africanus* 32, *P. dubius* 5, *P. simmondsi* 14). It

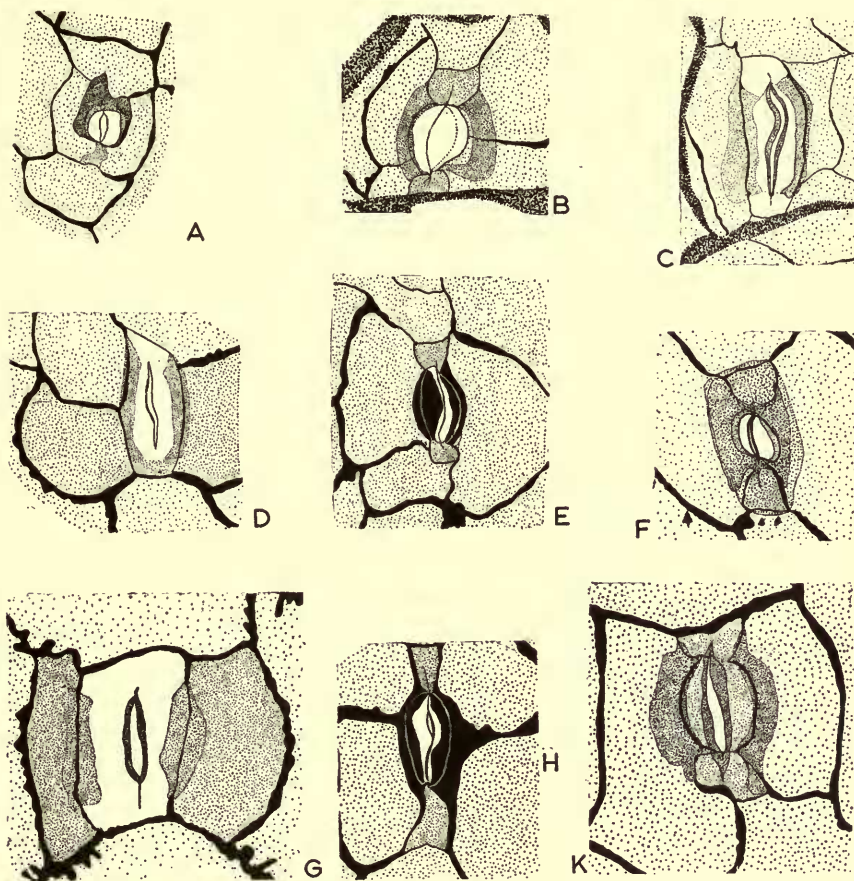


FIG. 8. *Pteruchus simmondsi*, *P. africanus*, *P. dubius*, *Dicroidium odontopteroides*, *D. feistmanteli*, *Xylopteris elongata*

A, E, *P. simmondsi*. Two stomata from same head on the same specimen showing (A) continuous cutin rim round stomatal pit, and covered guard cell poles, and (E) cutin flanges overhanging stomatal pit, and exposed guard cell poles. V.42687. B, C, *P. africanus*. Stomata from an upper (B) and a lower (C) head, each sort characteristic of the heads from which they come. V.42682. D, *P. dubius*. Stoma from a head near top of the sporophyll, of the sort most commonly met with in the species (cf. Fig. 10A). V.42683.

F, H, *X. elongata*. Comparable stomata to A and E, from under surface of same leaf. G, K, *D. feistmanteli* and *D. odontopteroides*. Stomata from the under surface of the leaves, each of the sort most commonly met with in their respective species.

All  $\times 650$ .

therefore seems very probable that the leaf of the same plant is still more abundant. Only those leaves represented by more than 20 specimens are considered. Though arbitrary, this limit does include all the common fossils. The residue consists of many more rare species usually represented by 10 or fewer specimens.

Table II summarizes the facts of association of *Pteruchus*. It will be seen that (i) the three leaves *Dicroidium odontopteroides*, *D. feistmanteli* and *Xylopteris elongata* have higher scores than any other leaf, and this impression is heightened by the fact that in four out of the five localities in which *D. feistmanteli* and *X. elongata* do not occur, *D. talbragarens* and *X. spinifolia* are recorded. These leaves are exceedingly like *D. feistmanteli* and *X. elongata* and have at times been merged with them (Jones & Jersey, 1947 : 15, 28). (ii) The only other leaves which rival the above three, are *Doratophyllum tenison-woodsii* and *Czekanowskia tenuifolia* both of which are known in gross form and cuticle, and can be discussed with some confidence. (iii) No further leaves, or group, comes near the *Dicroidium-Xylopteris* group, *D. tenison-woodsii* and *C. tenuifolia* in constancy of association.

The other associates of *Pteruchus* can be excluded on their cuticles. *Doratophyllum tenison-woodsii* (Jones & Jersey, 1947 : 37, 38, pl. 10, fig. 1) has straight cell outlines and stomata surrounded by a rather regular ring of 5 or 6 subsidiary cells whose inner edges overarch and form a rim above the stomatal pit. *Czekanowskia*

TABLE II.—*Pteruchus and its Associates*

Species	Localities												Total of associa- tions per species	Total local- ities 11
	Water- fall (over 20 speci- mens)	Ipswich Series localities (Jones & Jersey, 1944, pp. 65-71)										Rylance No. 3 Pit		
		19	20	21	29	31	34	36	39	39A				
<i>Dicroidium odontopteroides</i>	+	+	+	+	+	+	+	+	+	+	+	+	11	
<i>Dicroidium feistmanteli</i>	+	..	..	..	+	+	+	+	+	+	+	+	8	
<i>Xylopteris elongata</i>	+	+	+	+	+	..	+	+	+	+	+	..	9	
<i>Czekanowskia tenuifolia</i>	+	+	..	+	..	..	..	..	+	+	+	..	5	
<i>Doratophyllum tenison-woodsii</i>	..	..	+	+	..	+	+	+	+	+	+	..	7	
<i>Phoenicopsis elongatus</i>	+	..	..	..	..	..	..	..	..	..	..	..	1	
? <i>Stachyotaxus</i> sp.	+	..	..	..	..	..	..	..	..	..	..	..	1	
<i>Linguifolium lilieanum</i>	+	..	..	..	..	..	..	..	..	..	..	..	1	
<i>Lepidopteris stormbergensis</i>	+	..	..	..	..	..	..	..	..	..	..	..	1	
Taeniopterids (1)	+	..	..	..	..	..	..	+	..	+	..	..	3	
<i>Pseudoctenis</i> , <i>Zamites</i> and <i>Pterophyllum</i> group (2)	+	..	..	..	..	..	..	..	+	+	..	..	3	

(1) Comprises the "broad leaved Taeniopterids" viz. : *T. crassinervis*, *T. lata*, *T. immersa*, *T. wianamattae*, *T. dunstani* and *T. letriculiforme* (see Walkom, 1917 : 34-40 ; duToit, 1927 : 350-354, 401-403 ; Jones & Jersey, 1947 : 45-58).

(2) Comprises the leaves placed under *Pseudoclenis*, *Zamites* and *Pterophyllum* (in absence of information about the cuticle) by duToit, 1927 : 373-391 and Jones & Jersey, 1947 : 35-40.

In the absence of cuticle data I regard the separation of the above groups into species as nearly impossible.

*tenuifolia* (Jones & Jersey, 1947 : 59-61, pl. 6, fig. 2 and Text-fig. 6H) has at times been thought to be the leaf belonging with *Pteruchus* (p. 297), but its cuticle is different. It has straight cell outlines, and the stomatal aperture is (at least normally) orientated parallel with the long axis of the leaf. In *Pteruchus* the stomata are (at least usually) orientated obliquely or at right angles to the long axis of the organ

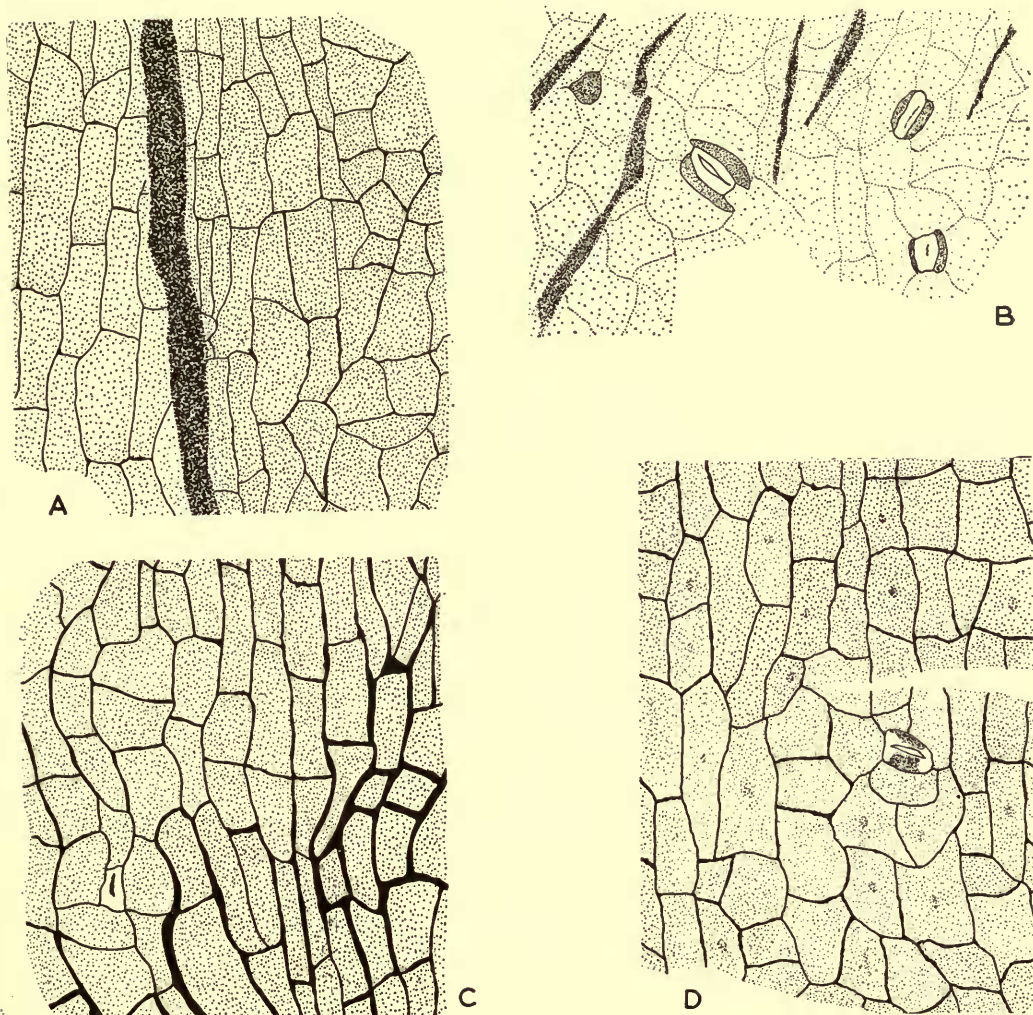


FIG. 9. *Pteruchus africanus*

A, cuticle from rachis margin (the line along which cuticle of the two surfaces joined slightly folded and shown in heavy stipple), showing elongated cells over marginal wing and different cell pattern on the two rachis surfaces (lower surface to left). B, cuticle from rachis upper surface, near top of sporophyll. C, D, two fragments of cuticle, originally opposite, from lower (c) and upper (D) rachis surfaces, showing different cell pattern on the two surfaces.

All V.42682.  $\times 250$ .



on the rachis and lack any preferred orientation on the heads. The stomata of *C. tenuifolia* are normally monocyclic, but those of *Pteruchus* dicyclic. In addition the *C. tenuifolia* from the Waterfall contains dense masses (? resin) in the leaf that are resistant to maceration, but nothing like this has been found in *Pteruchus*.

Of the other associates, the *Pseudoctenis-Zamites-Pterophyllum* and the taeniopterid groups have a very thin cuticle (probably less than  $0.5 \mu$ ) and so are unlikely to belong with a microsporophyll which has a thicker cuticle. The stomatal structure of these leaves is obscure, but it is less like *Pteruchus* than that of the *Dicroidium-Xylopteris* group. *Linguifolium lilieanum* (Jones & Jersey, 1947 : 48, 49) has such a delicate cuticle that I could not prepare it. *Lepidopteris stormbergensis* and *Phoenicopsis elongatus* each have stomata that are different from *Pteruchus* (Townrow, 1960 and Text-fig. 6A). The fossil called ?*Stachyotaxus* sp. (Kräusel, 1950) looks most like a conifer, and though it has stomata rather like those of *Pteruchus* it is, I think, unlikely to have anything to do with *Pteruchus*.

By the above arguments the leaves to which the three species of *Pteruchus* probably belonged are narrowed down to three, *D. odontopteroides*, *D. feistmanteli* and *X. elongata*.

It is not yet possible to say with much conviction which species of *Pteruchus* belongs with which leaf; the cuticles are too alike, and evidence from association is still slight. There are, however, small cuticle differences which suggest that *D. odontopteroides* and *P. africanus* (the commonest leaf and sporophyll), *D. feistmanteli* and *P. dubius* (the rarest) and *X. elongata* and *P. simmondsi* (intermediate as regards abundance) belong together. This suggestion is based on a comparison of cuticle of lamina and sporangial head. The cuticle of the rachises is nearly indistinguishable in both leaves and sporophylls, it lacks the distinctive form of the cell outlines and shows stomata often of somewhat anomalous form and degree of sinking.

In *D. odontopteroides* the central part of the cell outline is thin, but distinct, and the small sinuities tend to grade into the general cuticle so gradually that their exact outline is hard to see. In *D. feistmanteli* the central part of the outlines is thin but distinct and the sinuities are large, and distinct for most of their margins. In *X. elongata* the central part of the outline is wide but with indistinct edges, while the small sinuities are clearly marked off from the rest of the cuticle. The three species of *Pteruchus* show similar differences (Text-fig. 7).

In *D. odontopteroides* the stomata are normally sunken, but the stomatal pit is not overhung and the guard-cell poles exposed: the same is true of *P. africanus* (p. 298, Text-fig. 8B, C, K; Townrow, 1957, text-fig. 6). In *D. feistmanteli* and *P. dubius* the stomata are, at most, only slightly sunken, while there is a general thickening of the lateral subsidiary cells in about half the stomata seen (p. 297, Text-fig. 8D, G; Thomas, 1933, text-fig. 45; Townrow, 1957, text-fig. 9). In such specimens of *X. elongata* as I have examined and in those which have been adequately figured, the stomata are sunken and are either overhung by cutin flanges borne on the lateral subsidiary cells, or by a continuous cutinized margin of all the subsidiary cells, so that the guard cell poles (though partly cutinized) are covered. In *P. simmondsi* stomata with these features represent about three-quarters of all those seen (p. 305, Text-fig. 8A, E, F, H; Jones & Jersey, 1947, pl. 3, fig. 1).

However, the differences discussed above are slight and subject to variation (see p. 295); they cannot sustain the weight of much argument. It seems likely that evidence from repeated association is necessary before reference of leaf to sporophyll at specific level can be made convincing.

Frenguelli (1944) regarded the microsporophyll he called *Pterorrachis barrealeensis* (here *Pteruchus dubius*, p. 300), as belonging with the leaf he calls *Zuberia zuberi*. The evidence is restricted to the association of a single sporophyll with the leaves. The leaf called *Z. zuberi* is composite. Frenguelli has ignored cuticle data, but some of his figures show the thick leaf substance which is characteristic of the genus *Hoegia* and distinguishes it at once from *Dicroidium* (Frenguelli, 1944, pl. 9, figs. 1, 2; ? pl. 7, fig. 3): other figures are indistinguishable from *Dicroidium feistmanteli* (pls. 1, 4 & ?8, fig. 4). Others again are indeterminable on the information given. I accept the reference of Frenguelli's specimen to *Dicroidium feistmanteli*, but it is most unlikely that *Hoegia* has anything to do with *Pteruchus* or *Dicroidium*. It has a very thick leaf substance and a thick cuticle quite different from *Pteruchus* (Townrow, 1957: 47-51).

Frenguelli (1944a) records that the fossil he named *Stachyopitys anthoides* (here *P. simmondsi*) was found in a locality in the Estratos de Potrerillos where *X. elongata*, *Equisetites* and *Yabeiellia* spp. were common; but *D. odontopteroides* and *D. feistmanteli* are not mentioned. This may be additional evidence from association that *P. simmondsi* belongs with the leaf *X. elongata*, as is suggested on other grounds above (p. 312).

### (3) *The Morphology of Pteruchus*

Thomas (1933: 265; 1933a: 31, 40) has suggested that *Pteruchus* was a sporophyll, but by using the terms "axis", "bract" and "branch" (here rachis, pinnule and pinna) kept open the possibility that it was of stem-like nature, or a combination of leaf and stem. More evidence is now to hand, and I conclude that *Pteruchus* is best regarded purely as a sporophyll; i.e. that it is of leaf-like nature, and not like any other category of organ.

*Pteruchus africanus* is known to be borne directly on a stem in the manner of a leaf, and not in the axil of a leaf or bract (p. 292).

All three species show characters that are normal in leaves but not normal in stems, namely (1) They are built upon a pinnate plan throughout (pp. 290, 294); (2) they are dorsiventral and bilaterally symmetrical (pp. 290, 294); (3) the pinnae are offset towards the upper surface of the rachis like many (probably most) compound leaves, and certainly like the leaves *Dicroidium* and *Xylopteris* (Text-fig. 3D, E; Townrow, 1957: 28).

In two features the microsporophylls resemble the leaves to which they are referred but differ from the axes of the same plants: (1) the rachis cuticle is dorsiventral in microsporophyll and leaf, but is similar all over the axes (Text-fig. 6B, E, F); (2) the rachises of leaf and microsporophyll have a lateral wing, absent from the axes (p. 292).

The structures here called pinnules, but referred to as bracts or bracteoles by Thomas were what caused him to suggest that *Pteruchus* might possibly be of stem-

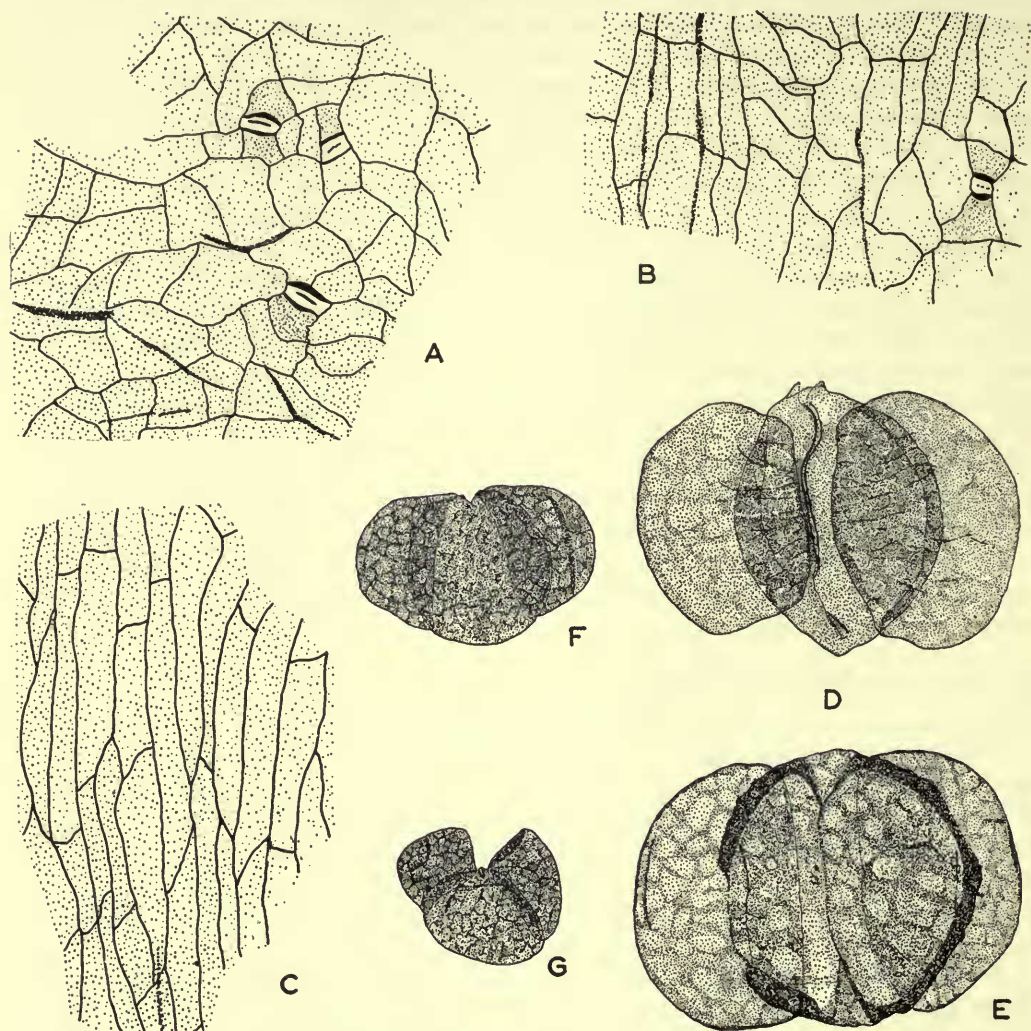


FIG. 10. *Pteruchus dubius*, *P. africanus*

A-C, *P. dubius*. A, cuticle from non-sporangial surface of head showing pattern of cells and stomata. V.42695.  $\times 250$ . B, c, cuticle fragments originally opposite, from upper (B) and lower (c) surfaces of rachis, showing difference in cell pattern and usual orientation of stomata. V.42695.  $\times 250$ . D-G, *P. africanus*. D, E, two pollen grains in distal (D) and proximal (E) polar views, showing sulcus and variation in shape and ornament of body and sacculi. From same sporophyll, but not same pollen sac. V.42689.  $\times 975$ . F, G, two pollen grains in tangential longitudinal view showing sulcus and variation of position of insertion of sacculi. From the same pollen sac. V.42688.  $\times 525$ .



like nature. The question is whether these organs are more like pinnules of a pinnate leaf, or bracts on an inflorescence. The reasons why they seem to me to be like pinnules and not bracts are as follows: (1) They are only produced occasionally, as might be expected of lower pinnules; but morphologically important organs like subtending bracts, or even bracteoles, should be constant. (2) No specimen has been seen which subtended a pinna, (or branch as it might be). (3) The pinnules set near the base of the microsporophyll have close agreement with a basal pinnule sometimes produced by leaves of the *Dicroidium-Xylopteris* group (Text-figs. 2A, B,

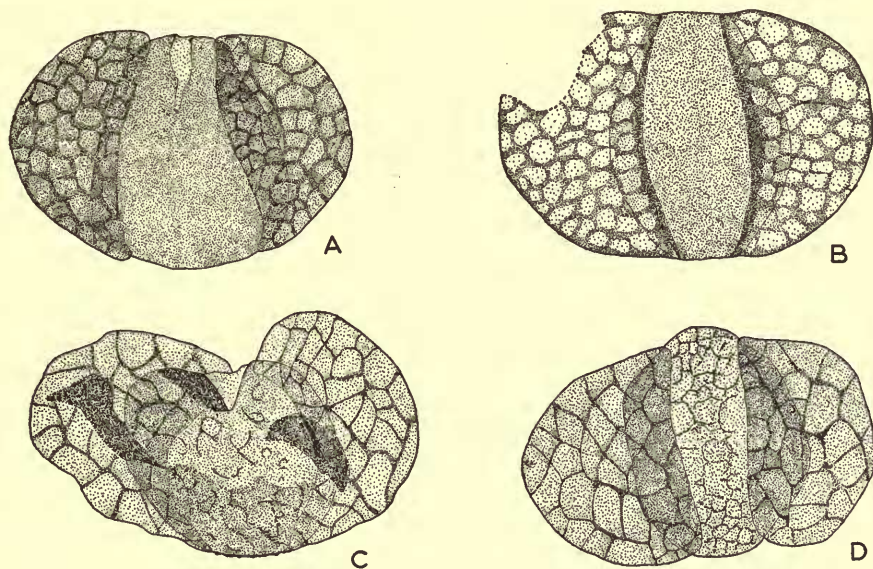


FIG. 11. *Pteruchus dubius*, *P. simmondsi*

A, B, *P. dubius*. C, D, *P. simmondsi*. Pollen grains in lateral (A, C) and proximal (B, D) polar views, showing body shape, insertion and ornament of sacculi. A, B, holotype, V.23389. C, D, V.42694. All  $\times 650$ .

5B, C). (4) The two alternately arranged pinnules near the sporophyll base in V.23360 (Text-fig. 3B) can easily be explained as reduced alternate pinnae; to regard them as bracteoles involves a number of assumptions (e.g. that the organ here called a sporophyll is part of a larger organ that has never been seen complete) which run contrary to other evidence, and have nothing to support them.

On the other hand, I can find no evidence that suggests that *Pteruchus* is a stem-like structure. Regarded as a sporophyll all the available evidence falls into a coherent picture; but regarded as any other sort of organ a number of points cannot be made to fit in, and must be dismissed arbitrarily as of no importance (Thomas, 1933 : 200).

Regarded as a sporophyll, the nature of the sporangial heads is easily explained. They are the distal portions of the pinnae, expanded into a lamina, bearing sori along the veins, the sori lacking a definite boundary, and becoming concrescent towards

the centre of the head. They are thus analagous to the sori of e.g. *Acrostichum aureum*. This view avoids the more complicated explanations, involving the possible presence of a cupule (an organ never satisfactorily defined, and of uncertain morphology) into which Thomas (1933 : 265) was obliged to enter.

At present I express no views upon possible homologies between the parts of *Pteruchus* and of *Umkomasia* and its allies, though, like Thomas, I believe they belonged to the same plants.

#### (4) *Comparisons and Taxonomic Position*

A full discussion of the taxonomic position of the Corystospermaceae must wait until their seed-bearing organs are reconsidered. At present *Pteruchus* is compared with various other pollen organs to clear the ground for such a wider discussion. Here the older and usually more inclusive terms Pteridospermae (= Cycadofilicales), Lyginopterideae, Medulloseae and Corystospermaceae are used in preference to any of the more recent alternatives (Pant, 1957). This is for two reasons. The first is that for the present purpose, the older terms are more useful. The second is that the fundamental point—the morphology of the seed-bearing organs of the Corystospermaceae—is not yet satisfactorily decided. Thomas (1933 : 256) describes them as inflorescences, but points out several facts inconsistent with this view : until these organs are re-examined and their morphology decided, the Corystospermaceae cannot be classified otherwise than as a family *incertae sedis*.

A difficult point in comparing *Pteruchus* is that there is no evidence suggesting which way evolution within the genus has gone. Taking different basic premises any of the species could be called the most primitive, and the others derived from it, or all could be considered equally advanced, derived independently from a common (hypothetical) ancestor. Accepting the suggested ascriptions to the leaves (pp. 312, 313) it is not clear which is the older (Jones, 1949 ; Jones & Jersey, 1947 : 73), hence this line of argument does not help.

Thomas regarded the Corystospermaceae as belonging to the Pteridospermae. I agree entirely, if we define the Pteridospermae as "gymnospermous plants with leaves, pollen- and seed-bearing organs pinnate. Reproductive structures not aggregated in cones or flowers".

*Pteruchus* has been compared with *Crossothea* (Kidston, 1923 ; Remy, 1956) by Thomas (1933 : 256). They are alike in two respects : both are pinnate and bear the pollen sacs on what is most reasonably regarded as a modified pinna or pinnule. Otherwise they are different ; differing in the manner of insertion of the pinna petiole, the way in which the pollen sacs are arranged, and in that *Crossothea* (at least the better known species) has bilocular synangia. *Crossothea* is regarded as belonging to a lyginopterid plant (Jongmans, 1950).

There is some resemblance between *Pteruchus* and *Potoniea* (Halle, 1933 ; Remy, 1956) for both bear long, free, unilocular sporangia, dehiscing by a longitudinal slit, toward the centre of a cup-like pinnule with a lobed or dentate margin. *Potoniea* is attached basally, and the pollen differs.

Thomas (1933 : 254) also compared *Pteruchus* with *Dictyothalamus schrollianus* W. & R. Remy, 1958). There are a number of most interesting similarities. *D.*

*schrollianus* is pinnate, and may be forked, and the rachis is lumpy, at any rate in some specimens, like *Pteruchus*. The pollen sacs are massed over one surface of the "head", and the pinna appears to be inserted on, or mostly on, the sporangial side, and its continuation on to the "head" is free of pollen sacs. The pollen sacs probably lie in rows, as may be so in *Pteruchus*. The comparison cannot be pressed too far. The pollen of *D. schrollianus* is monosaccate, while the structure of the "head" and pollen sac is unknown. *D. schrollianus* is of unknown affinities. Its pollen is like that of *Schuetzia anomala* (Remy & Rettschlag, 1954; W. & R. Remy, 1958) but otherwise the two organs appear to be rather different.

Two Rothliegend fossils, *Pteridospermostrobus gimmianus* Remy (1954) and *Manebachia polysporangiata* W. & R. Remy (1958a) bear superficial resemblance to *P. simmondsi* and *P. dubius*, but differ in structure. *Thuringia callipteroides* Remy (1953) has bisaccate pollen like *Pteruchus* but is otherwise quite different. According to Potonié & Kremp (1956) the pollen of *T. callipteroides* is monosaccate, however.

*Pteruchus* shows no point of approach to any Medullosean pollen organ (Halle, 1933), neither is it like any of the fructifications belonging to *Glossopteris* and *Gangamopteris* (Plumstead, 1959, discussion). It differs widely from those fossils found associated with *Glossopteris* (Thomas, 1958; Pant, 1958), except that it has bisaccate pollen.

There are no Mesozoic fossils that can be closely compared with *Pteruchus*. Among the supposed pteridosperm derivatives *Caytonanthus* (Harris, 1950, discussion) is pinnate and has bisaccate pollen like *Pteruchus*. *Caytonanthus* bears a radially symmetrical group of (usually) four pollen sacs, pendulous from an unexpanded branchlet end of the sporophyll, which dehisces by the pollen sacs splitting apart from one another. These features are quite different from anything seen in *Pteruchus*, and, in detail the pollen is different; *Caytonanthus* pollen is about 15  $\mu$  wide, and has a scarcely visible sulcus, but *Pteruchus* pollen is about 70  $\mu$  wide, and shows a distinct sulcus.

*Antevsia* the pollen organ of the Peltaspermeaceae (Townrow, 1960) resembles *Pteruchus* only in being pinnate and in having pollen sacs that dehisce by a longitudinal slit. Otherwise it differs markedly. The pollen sacs are either borne marginally on a disc, or on the under surface, possibly opposite on marginal lobes, of a fertile branchlet of the sporophyll. The pollen sacs are massive, with stomata, and probably with vascular tissue. The pollen is monosulcate.

Four other Triassic fossils have bisaccate pollen rather like *Pteruchus*. They are: *Harrisiothecium marsiloides* (Harris, 1935; Lundblad, 1950) which branches in all three planes, and has a two-valved synangial pollen-bearing portion with immersed pollen sacs, one row in the tissue of each valve. It is thus widely different from *Pteruchus*. *Pamelreuthia halberfelneri* (Kräusel, 1948) which is pinnate, but differs in having pollen sacs, probably one row, sunken in the tissue of the expanded pinna ends, so forming synangia. *Ruhleostachys pseudoarticulatus* Roselt (1956) which is an organ of entirely different structure from *Pteruchus*, probably very close to the conifers, and the conifer *Voltzia* (?) *heterophylla* (Wills, 1910; Couper, 1958), which is clearly unconnected with *Pteruchus*.



It has been suggested (Thomas, 1933 : 260) that *Pteruchus* is comparable with a catkin, e.g. of *Populus*, but since *Pteruchus* is a sporophyll this comparison cannot be maintained.

In conclusion, the genus *Pteruchus* cannot be exactly classified. It resembles a number of fossils in being pinnate, or having bisaccate pollen, or pollen sacs that dehisce by a longitudinal slit ; but these are all characters which are shared by a wide range of plants otherwise dissimilar. The bisaccate pollens, for example, are very numerous and all rather similar (see Potonié, 1958). As far as evidence from the pollen organs goes, *Pteruchus* is remote from any of the " Mesozoic Pteridosperms " (including, for convenience only, the Caytoniales), indeed, as far as they are known, each of the " Mesozoic Pteridosperms " is remote from the others. The evidence (and it is far from complete) suggests that they are so different that they are best placed in different orders (but see Gothan & Weyland, 1954). Among the Palaeozoic pteridosperms comparison is possible, though never close, between *Pteruchus* and pollen organs in which the pollen sacs were borne on a laterally attached pinnule. This seems to have been a character of the Upper Carboniferous Lyginopterideae (if indeed *Crossothea* did belong to a lyginopterid plant), and so suggests some connection with the Lyginopterideae. The differences between *Pteruchus* and any lyginopterid fossil indicate the connection is remote.

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## PLATE 24

*Pteruchus simmondsi* (Shirley)

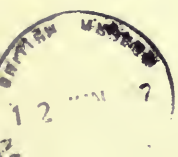
- FIG. 1. A sporophyll showing alternate branching. V.42681.  $\times 2$ .
- FIG. 2. The holotype. Queensland Geological Survey No. F.256.  $\times 2$ .
- FIG. 3. The lower portion of the sporophyll shown in Fig. 1, showing form of sporangial heads and of the pinnae.  $\times 6$ .

*Pteruchus africanus* Thomas

- FIG. 4. A sporophyll (in transfer) seen from the upper surface. V.42682.  $\times 2$ .

*Pteruchus dubius* Thomas

- FIG. 5. A sporophyll. V.42683.  $\times 2$ .
- FIG. 6. Base of the same specimen, showing basal pinnule (right), ? fragment of axis (left) and first pinna with pinnule just above its insertion (cf. Text-fig. 4c).  $\times 7$ .







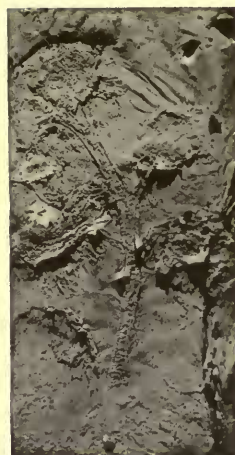
1



6



2



4



5



3







PLATE 25

*Pteruchus africanus* Thomas

FIG. 1. Lower portion of a sporophyll showing single pinnule about midway between sporophyll base and first pinna. V.42684.  $\times 6$ .

FIG. 2. Portion of axis (horizontal) and base of a sporophyll (curving to run vertically). Photograph taken under  $\text{NH}_4\text{Cl}$ ; illuminated from bottom left. V.42685.  $\times 6$ .

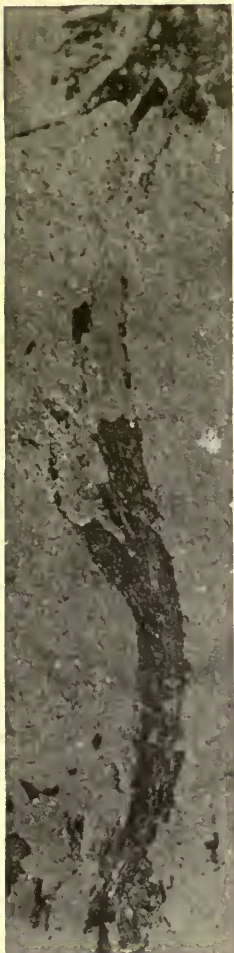
*Pteruchus dubius* Thomas

FIG. 3. A sporangial head, sporangial surface exposed, showing insertion of pinna, marginal lobes devoid of pollen sacs (next pinna insertion and at distal end) and pollen sacs over rest of the surface. V.42686.  $\times 6$ .

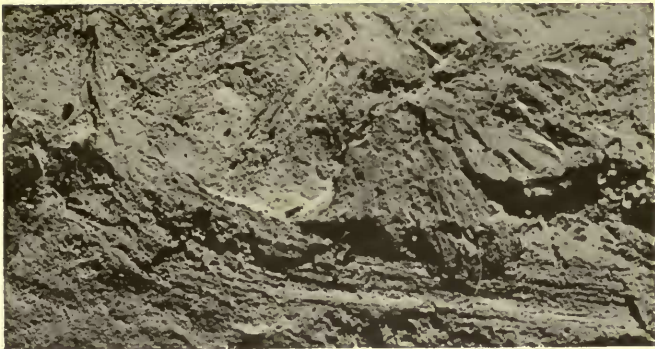
*Xylopteris elongata* (Carruthers)

FIG. 4. The base of a leaf showing long but undivided basal pinnule (cf. Text-fig. 5B).  $\times 6$ .

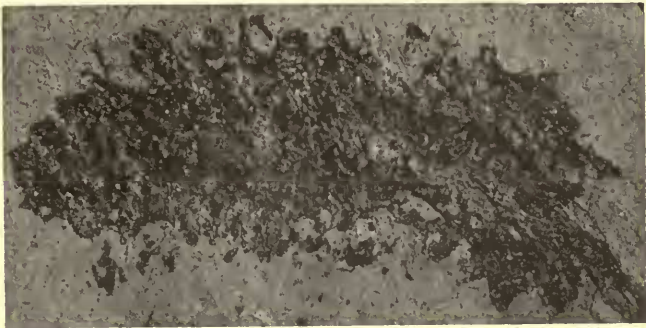
FIG. 5. A leaf base attached to a short piece of axis (running to right).  $\times 6$ .



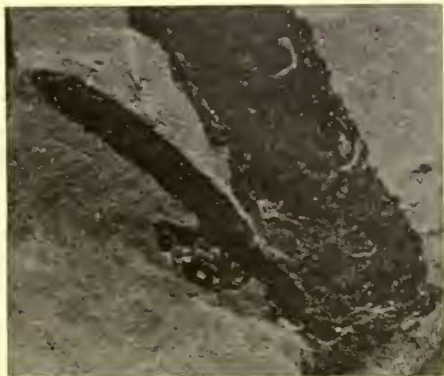
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4



5







PLATE 26

*Pteruchus dubius* Thomas

FIG. 1. Pollen grain, polar view distal face, showing sulcus. An abnormally small specimen. V.23389.  $\times 500$ .

*Pteruchus africanus* Thomas

FIG. 2. Pollen grain, tangential longitudinal view, showing sulcus in optical section and insertion of sacchi. V.23384.  $\times 500$ .

FIG. 4. Pollen grain, polar view distal face, showing sulcus. V.23384.  $\times 500$ .

FIG. 5. Section of a pollen sac showing single loculus. V. 42688.  $\times 260$ .

FIG. 6. Sporophyll base showing a single pinnule and an impression of another or (?) of part of the axis. V.23385.  $\times 9$ .

FIG. 7. The cuticle of the edge of a head showing small foldings and cuticle extending as a rim on to sporangial surface (at *a*).

FIG. 8. A head, showing the rugose (non-sporangial) surface. V.42682.  $\times 7$ .

FIGS. 9, 10. Two heads, sporangial surface seen free of pollen sacs, showing area of pollen sac attachment, and ridges marking course of veins. Note margin and lobes smooth, and in Fig. 9 little rings running more or less parallel with a vein. Photographs taken under  $\text{NH}_4\text{Cl}$ , illuminated from bottom left. V.23394.  $\times 7$ .

FIG. 11. Part of pollen sac wall (in transfer) showing single layer of cells forming the wall at maturity. V.42690.  $\times 50$ .

*Pteruchus simmondsi* (Shirley)

FIG. 3. Pollen grain, polar view distal face, showing sulcus. V.42687.  $\times 500$ .

FIG. 12. A head, sporangial surface exposed, showing pinna insertion and large marginal lobes. V.42681.  $\times 7$ .



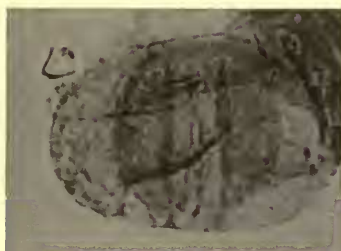
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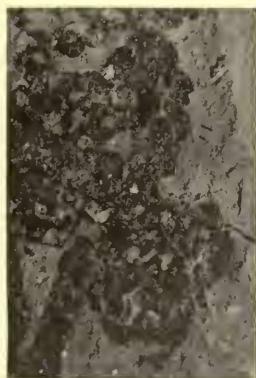
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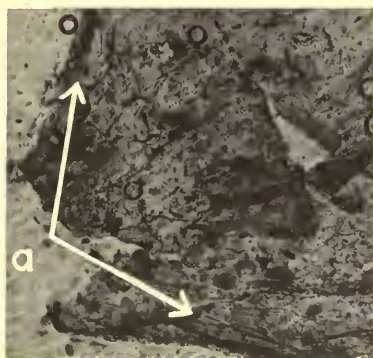
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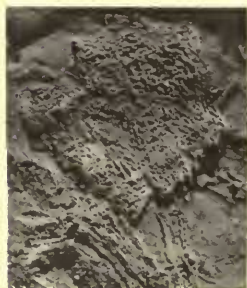
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12



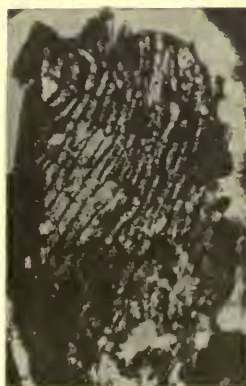
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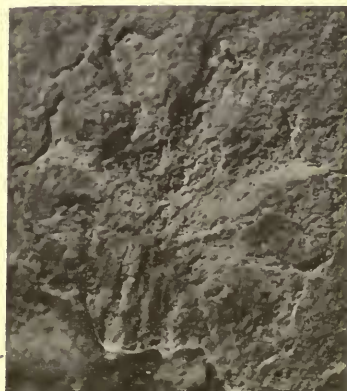
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